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THE MOVEMENTS AND REACTIONS OF THE ISOLATED MELANOPHORES OF THE FROG

BY

S. J. HOLMES

The observations previously reported by me (1913) on the movements of isolated pigment cells derived from the embryos and young larvæ of amphibians showed that these cells undergo marked changes in outline, and frequently creep for a considerable distance away from the tissue in which they were embedded. The hanging-drop cultures in which these cells were studied presented exceptionally favorable conditions for observation which rendered it possible to determine, without the least uncertainty, that the pigment cells changed in an amoeboid fashion, that the processes of ectoplasm that were formed were very quickly invaded by pigment granules, and that the distribution of pigment within the cell gave a fairly faithful picture of the outline of the cell itself. The old question as to whether the changes that may be observed in pigment cells are due to changes in the outline of the entire cell or to the flow of pigment within cell processes which remain comparatively unchanged is therefore to be decided, for the forms studied at least, in favor of the former view.

It would not be safe, however, to draw the same conclusion in regard to the pigment cells of the adult animals, especially since so many investigators have convinced themselves of the opposite interpretation. Studies of the behavior of pigment cells of other animals in places such as the transparent fins and tails of fishes where they could be readily observed, have led several observers to the conclusion that pigment may flow back and forth within processes of pigment cells which may be followed more or less clearly despite their transparency. Following the cell processes of a chromatophore when they are devoid of pigment is usually very difficult, and in most cases

impossible when the chromatophore is surrounded by other cells. The difference of opinion regarding the movement of chromatophores which this difficulty occasioned has persisted even down to the present time, although the majority of investigators now consider the expansion and concentration of pigment within the chromatophore as the principal factor in the changes observed. Gaupp (1904), for instance, in his excellent revision of Ecker and Wiedersheim's *Anatomie des Frosches*, states:

Nach der schon lange von verschiedenen Seiten ausgesprochenen und neuerdings gut begründeten Anschauung handelt es sich dabei nur um scheinbare Bestaltveränderungen, in Wirklichkeit um eine verschiedene Vertheilung der Pigmentkörnchen innerhalb der Zellen. Die verästelten Fortsätze der Zellen sind bleibende, constante Theile derselben, in denen jedoch ein Strömen des Farbstoffkörnchen stattfinden kann. Es kann also einerseits eine Retraction des Pigmentes aus den Fortsätzen und Concentration desselben im Zellkörper, ja sogar nur in einem centralen Gebiete dasselben, erfolgen: alsdann sind die Fortsätze pigmentfrei, blass und können bei der Untersuchung unerkant bleiben, so dass die Pigmentmasse eine rundliche in sich abgeschlossene Form erhalten muss (Pigmentballung); anderseits können die Pigmentkörnchen in die feinsten Verzweigungen der Fortsätze ausströmen und dadurch diese hervortreten lassen: Pigmentexpansion.

Although my observations on the isolated chromatophores of amphibian larvae showed that the more prevalent interpretation did not apply to the particular species studied, later investigations of the isolated chromatophores of the adult frog revealed certain conditions more in accord with this interpretation, although showing at the same time its untenability in other respects.

Pieces of tissue containing pigment cells were cut up in Ringer's solution and mounted in a hollow slide in a hanging drop of lymph. If the lymph coagulated, some of the pigment cells would wander out, either in contact with the cover slip, or, more frequently, along the free surface of the drop. The observations concerned only the black pigment cells or melanophores of the frog, as the other varieties of chromatophores did not isolate themselves in any of the preparations. The most favorable source was the pigmented peritoneum occurring along some of the veins of the anterior part of the body. The largest melanophores did not wander out, and of the pigment cells that isolated themselves, the smaller ones were, as a rule, the more active. Like epithelial cells, the melanophores showed a marked thigmotaxis, although they did not manifest so strong a tendency to become flattened out as is exhibited by most cells of epithelial origin.

The movements of the smaller melanophores are very much like those of an *Amoeba*. Pseudopods are thrust out and retracted, and often broad, thin sheets of protoplasm may be extended from the cell. In several cases a considerable amount of migration was observed; in one instance this amounted to over ten times the diameter of the cell. When first formed, the pseudopods appear as a thickening of clear ectoplasm which may, however, be very quickly invaded by endoplasm containing black granules of pigment. In many cases the pseudopod may reach a considerable size before it comes to contain any pigment granules, and often broad sheets of protoplasm may be thrust out, in which pigment is almost entirely absent. The forms assumed by the melanophores are very varied. In the larger pigment cells the processes are generally more numerous, relatively longer, and more branched. The pseudopods of the larger cells may be several times the diameter of the body of the cell, which they seldom are in the smaller ones. They may contain pigment nearly to the extreme tip, or they may be almost entirely devoid of it, different processes of the same cell presenting great differences in this respect.

The pigment cells of the adult frog differ therefore from those of the young larvae in that they frequently possess transparent processes. To a certain degree pigment may flow back and forth within these processes. But the largest factor in determining the changes in pigment distribution, especially in the smaller melanophores, is the change in the outline of the cells themselves.

The behavior of advancing pseudopods indicates that they are not pushed out, but pulled out. The Pseudopods that are being extended are not blunt and evenly rounded as they would be if pushed out by the pressure of the endoplasm. When the pseudopod is broad the ectoplasm at the advancing extremity is commonly in the form of a broad, thin sheet with very fine processes of transparent protoplasm. These processes are closely applied to the substratum to which they adhere. This thin, transparent region of protoplasm is the chief seat of locomotor activity. The part lying behind it is apparently pulled along by the contractility of the ectoplasm. The end of an advancing pseudopod is commonly broader and thinner than the region lying behind it. A certain tendency to spreading at the extreme end usually characterizes also the very long and narrow processes that sometimes appear. The proximal part may then be nearly cylindrical and almost uniform in diameter and gives every appearance of having been pulled out. When the pseudopod is retracting, the tip is commonly

blunt and the proximal part often becomes irregular in contour. Other tissue cells, especially those of the peritoneal epithelium, frequently produce pseudopods which greatly exceed in length and tenuity those which arise from the melanophores, and the method of their formation is clearly the same as that just described. The enlargements at the end of the outgrowing nerve fiber, which were observed by Harrison (1910) in living neuroblasts, and which have been found in stained preparations by various writers, have also much the same character. In these cases, as in the extension of sheets of ectodermic epithelium, the hyaline amoeboid protoplasmic tip or border of the advancing cells appears to be the active region which is responsible for the progressive movement.

Unfavorable conditions cause the pseudopods to be withdrawn and the pigment cell to assume a more rounded contour. The fine processes of the transparent ectoplasm do not appear, and the cell becomes quiescent. Exposure to a higher temperature tends to produce a contracted condition of the cells, but the reaction is not marked short of a temperature which is injurious.

Several experiments were performed to ascertain if the pigment cells would respond to light. Inasmuch as light has been described as having a blanching effect upon excised pieces of frog's skin it was thought probable that a direct effect on the isolated melanophores might be demonstrable. In all the experiments with light the heat was screened out by passing the light through several inches of cool water. A sharply defined beam of strong light was thrown on one part of an active melanophore, but even continued exposure failed to show that the reactions of the exposed part were in any way different from those of the shaded region of the cell. Pigment cells would remain expanded for over an hour in the strong glare of direct sunlight which the unprotected eye could scarcely endure. One active melanophore was alternately exposed to the intense light of an arc lamp and to darkness for the greater part of a day, and was sketched at regular intervals of twenty minutes. On the average the sketches after exposure to light did not show that there was any greater tendency to contract in the light than in the dark. Since the cell usually changed considerably in outline between successive sketches, if there were any marked tendency to contract or to expand under the influence of light it would probably have become manifest. The light used in this experiment was so strong that the object could be observed only through smoked glass held over the eye-piece of the microscope. Other

experiments with strong as well as with less intense light yielded the same negative result. It may be that light has some direct effect on the form of isolated melanophores, but its influence, if it has any, is not strong.

From what has been said, the melanophores of the frog show an evident positive thigmotaxis which is different in its manifestations from the thigmotaxis of ectodermic epithelium and various other kinds of tissue cells. An important element in the extension of the pigment cells as well as other kinds, is, I believe, the adhesiveness of the protoplasm of the newly formed fine pseudopods. In one instance a pigment cell which had partly crept out of a sheet of extending epithelium had sent out a large process which was apparently attached at its end to the cover slip. While the cell was being observed the sheet of ectoderm contracted carrying the base of the pigment cell away. The tip of the cell remained attached so that the cell became pulled out to several times its previous diameter, when finally it loosed its hold and the cell quickly contracted to nearly its original form. The same adhesiveness is shown in the pseudopods of *Amoeba* and other rhizopods, and probably plays an important rôle in amoeboid movement in general.

SUMMARY

Black pigment cells of tissues from the frog cultivated in lymph or plasma sometimes wander out free from other cells. The pigment cells show a typical amoeboid movement and may creep to a considerable distance.

The smaller melanophores are relatively more active and become isolated more often than the larger ones.

Processes may be formed that are mostly free from pigment, and pigment may flow back and forth within cell processes so that changes in the distribution of pigment in the chromatophores are partly due to the variation in the distribution of pigment within the cell, and partly due to changes in the outline of the cell itself.

Heat causes a withdrawal of cell processes.

Light has very little influence in the movements or state of contraction of the melanophores.

Pigment cells show a positive thigmotaxis, the newly formed pseudopods being adhesive to solid bodies.

NOTE.—On the day in which the proof of the present article came from the printer, a paper was received from Dr. Davenport Hooker (1914) on amoeboid movement in the melanophores of the frog. The melanophores were studied partly by means of sections of preserved material and partly by observation of the living but not isolated cells. Hooker's results arrived at by different methods are quite in accord with my own, and lead him to the conclusion that "The melanophores of both larval and adult frogs expand and contract within the spaces which enclose them. As the processes of expansion and contraction are performed by means of pseudopodia, these cells are amoeboid."

Transmitted March 31, 1914.

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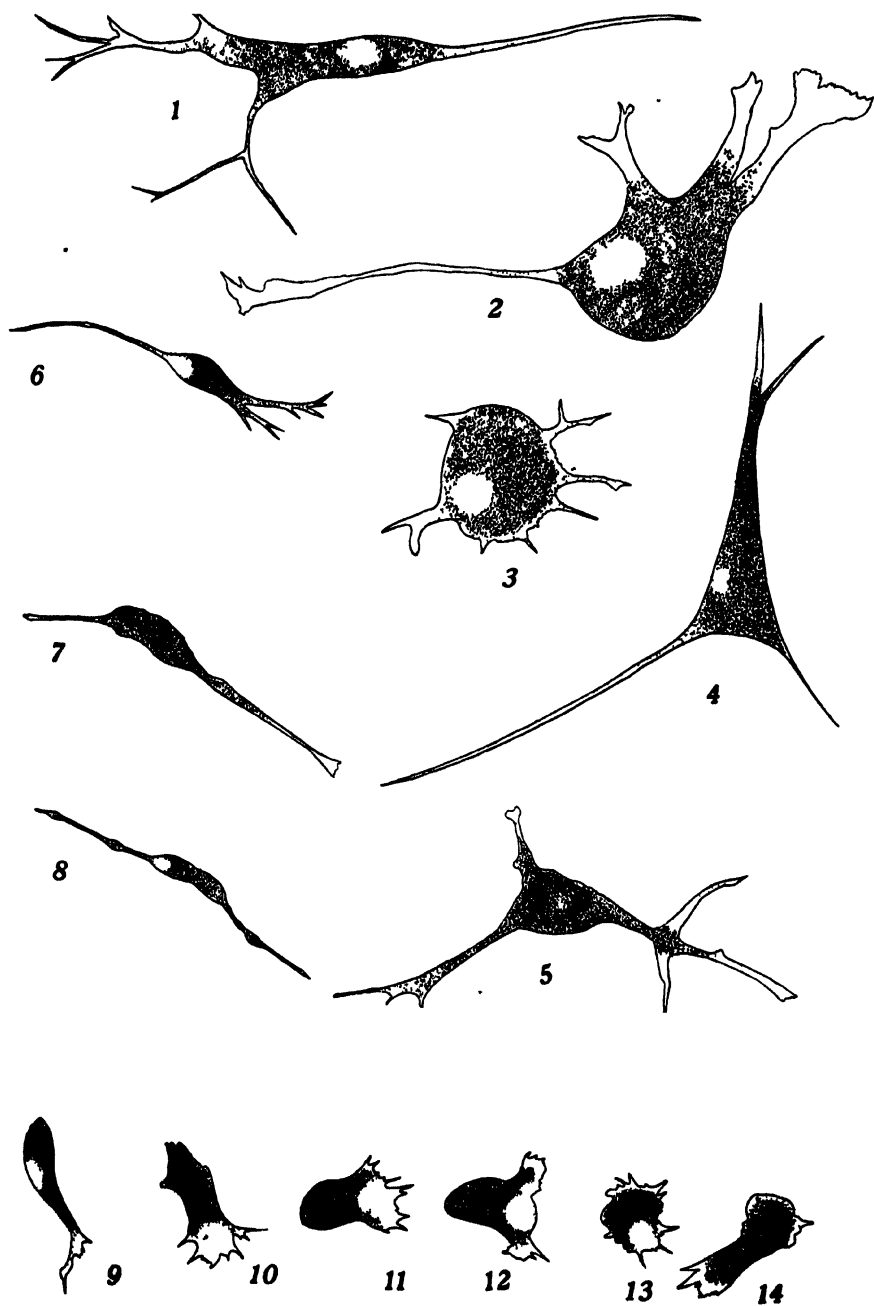
EXPLANATION OF PLATE 10

All of the figures were drawn to the same scale and represent isolated pigment cells from the frog *Rana pipiens*.

Figs. 1-5. Various forms of the larger pigment cells that became isolated in the culture medium.

Figs. 6, 7 and 8 were taken at different times from the same cell.

Figs. 9-14 represent successive changes in form of a single cell within a half hour.



POLYCHAETOUS ANNELIDS OF THE PACIFIC
COAST IN THE COLLECTIONS OF THE
ZOOLOGICAL MUSEUM OF THE
UNIVERSITY OF CALIFORNIA

BY

AARON L. TREADWELL

The following paper contains a list of old, and a description of a few new species of Pacific polychaetous annelids belonging to the University of California which, through the courtesy of Professors W. E. Ritter and C. A. Kofoid, were submitted to me for study. As a result of the earlier papers of Johnson, and the later elaborate work of Moore, our knowledge of the Pacific coast Polychaeta is very complete and I was prepared to find, what proved to be actually the case, that the greater number of the specimens submitted to me had already been described.

Twelve new species were found in the collections and are here described: *Panthalis pacifica*, *Nereis notomacula*, *Spio acuta*, *Scolecoplepis alaskensis*, *Polydora californica*, *Streblosoma crassibranchia*, *Trophonia minuta*, *T. inflata*, *Ophelina magna*, *O. mucronata*, *Laonome oculifera*, and *Branchiomma disparoculatum*.

While it was not my original intention to do more than publish a description of these new species, I have, at the request of Professor Kofoid, included all of the old, with the intention of thus securing a more complete and easily accessible list of the localities from which the various species were collected, as well as a record of whatever data concerning depth of water and character of bottom were available. The collections included some material from Honolulu and from localities along the coast as far north as Alaska, as well as

material obtained with trawl and tow-net during the explorations of the Marine Biological Station of San Diego. Localities relative to the former are entered in sequence from north to south and those relative to the latter according to the haul numbers under which the collections are accessioned (see Ritter, 1914).

Family SYLLIDAE

Syllis heterochaeta Moore

Syllis heterochaeta Moore (1909b), p. 322, pl. 15, figs. 1-4.

Moore described six eyes for this species. These, which agreed with his description in other respects, had only four. Another difference from Moore's description was that the setae instead of being simply rounded had a subterminal depression.

Collected from Bolinas Bay.

Syllis alternata Moore

Syllis alternata Moore (1908b), p. 323, and (1909b), p. 321.

Collected from Ocean Cape, Yakutat Bay, Alaska; near Black Point, San Francisco Bay; Pacific Grove; and San Pedro.

Syllis armillaris Oersted

Syllis armillaris Oersted (1843b), p. 24, figs. 90, 94, 102.

Collected from Point Loma; and San Diego.

Syllis (Pionosyllis) elongata Johnson

Pionosyllis elongata Johnson (1901), p. 403, pl. 6, figs. 67-70; pl. 7, fig. 71.

Collected from Dillon's Beach; Black Point, San Francisco Bay; Pacific Grove; Monterey; San Pedro; and Pillar Point, Calif.

Pionosyllis gigantea Moore

Pionosyllis gigantea Moore (1908b), p. 325.

Collected from Bolinas Bay; and in haul LXVII, off San Diego in 19 to 31 fathoms on grayish-yellow sand; one specimen from an unknown locality.

Trypanosyllis intermedia Moore

Trypanosyllis intermedia Moore (1909a), p. 236, pl. 7, figs. 1, 2.

Collected from San Pedro and San Diego, and also in haul LXXVIII, from the piles of the Santa Fé wharf in San Diego Bay.

Trypanosyllis gemmipara Johnson

Trypanosyllis gemmipara Johnson (1901), p. 405, pl. 7, figs. 72-76.

Locality unknown.

Odontosyllis phosphorea Moore

Odontosyllis phosphorea Moore (1909b), p. 327, pl. 15, figs. 8-10.

Collected from Bolinas Bay; Monterey; Pacific Grove; Avalon. Santa Catalina Island; and Coronado.

One mutilated specimen, from an unknown locality, agreed in general with Moore's description, but had five prominent longitudinal lines on the dorsal surface. Notopodial setae from the middle of the body are very long, delicate, flat, gently tapering to the end.

Odontosyllis sp. (?)

Collected from San Pedro.

Family HESIONIDAE

Podarke pugettensis Johnson

Podarke pugettensis Johnson (1901), p. 397, pl. 3, figs. 23-25.

Collected from Port Orchard and Alki Point, Puget Sound.

Podarke sp. (?)

Collected from San Diego.

Family APHRODITIDAE

Aphrodita refulgida Moore

Aphrodita refulgida Moore (1910), p. 376, pl. 32, figs. 76-84.

Collected in haul VI-1, off San Pedro in 10 to 24 fathoms on gray sand and mud, and in haul XIX-1, off San Pedro in 30 to 102 fathoms on soft mud, sand, and pebbles.

Aphrodita castanea Moore

Aphrodita castanea Moore (1910), p. 380, pl. 32, figs. 85-97; pl. 33, fig. 98.
Collected at 160 fathoms (locality ?).

Aphrodita parva Moore

Aphrodita parva Moore (1905a), p. 529, pl. 34, figs. 3-7.

Collected in the following hauls: XIV-1, off San Pedro in 40 to 155 fathoms on soft, sticky mud; XXVII-2, off Santa Catalina Island in 16 to 40 fathoms on fine gray sand and green mud; XLIII-1, in San Diego Bay in 3 to 7 fathoms on soft, black mud; LV-1, off San Diego in 23 to 26 fathoms on mud and sand; LXV, in San Diego Bay in 3 fathoms on sand and eel-grass.

Aphrodita negligens Moore

Aphrodita negligens Moore (1905a), p. 526, pl. 34, figs. 1-2; pl. 35, fig. 31.

Collected in haul LVIII, off the Coronado Islands in 15 to 18 fathoms on sand and shells; and in haul 6, off San Diego in a net towed at 90 fathoms.

Family AMPHINOMIDAE**Euphrosyne heterobranchia Johnson**

Euphrosyne heterobranchia Johnson (1901), p. 402, pl. 6, figs. 60-66.

Collected from Kodiak Island, Alaska.

Euphrosyne aurantiaca Johnson

Euphrosyne aurantiaca Johnson (1897), p. 157, pl. 5, figs. 1-4.

Collected from Santa Monica; Portuguese Bend; and San Diego.

Euphrosyne hortensis Moore

Euphrosyne hortensis Moore (1905a), p. 534, pl. 34, figs. 13-16.

Collected from Blunt's Reef; and in haul LXVII, off San Diego in 19 to 31 fathoms on grayish-yellow sand.

Euphrosyne arctica Johnson

Euphrosyne arctica Johnson (1897), p. 159, pl. 5, figs. 5-7.

Collected from San Pedro; and in haul LXX-2, off La Jolla in 51 to 98 fathoms on rocky shale.

Eurythoe californica Johnson

Eurythoe californica Johnson (1897), p. 159, pl. 5, figs. 8-14.

Collected from Pacific Grove; San Pedro; La Jolla; and San Clemente Island.

Amphinome rostrata Pallas

Amphinome rostrata Pallas (1766), p. 106, pl. 8, figs. 14-18.

Amphinome rostrata, McIntosh (1885), p. 21, pl. 1, fig. 7; pl. 4, fig. 1; pl. 1a, fig. 16; pl. 2a, figs. 8-12.

Locality unknown.

Chloeia euglochis Ehlers var. ?

Chloeia euglochis Ehlers (1887), p. 18, pl. 1, figs. 1-2; pl. 2, figs. 1-8; pl. 3, figs. 1-4.

Locality unknown.

Hermodice pennata Treadwell

Hermodice pennata Treadwell (1906), p. 1165, fig. 41.

Locality unknown.

Family PALMYRIDAE

Chrysopetalum occidentale Johnson

Chrysopetalum occidentale Johnson (1897), p. 161, pl. 5, figs. 15, 16; pl. 6, figs. 17-19.

Johnson's type-specimen was collected from San Pedro. Another specimen in the collection came from San Diego.

Family POLYNOIDAE

Halosydna interrupta v. Marenzeller

Halosydna interrupta v. Marenzeller (1902), p. 570, pl. 1, fig. 2.

Polynoe semierma, Moore (1903), p. 402, pl. 23, figs. 2-3.

Halosydna interrupta, Moore (1910), p. 331.

Collected from San Pedro and also in the following hauls: LXX-7, off La Jolla in 55 to 125 fathoms on soft black shale; LXXXIII, off Point Firmin in 60 to 130 fathoms on sand and broken shells.

Halosydna pulchra Johnson

Polynoe pulchra Johnson (1897), p. 177, pl. 7, figs. 34, 43, 43a; pl. 8, figs. 50, 50a, 50b.

Collected from Pacific Grove, San Pedro, Ballast Point (San Diego), and in the following hauls: XIV-3, off San Pedro in 40 to

150 fathoms on gray mud; XLVII-1, off Coronado in 8 to 10 fathoms on sand and eel-grass; LXVI, in San Diego Bay in 7 to 9 fathoms on sand and broken shells; LXXII-1, off San Diego in 46 to 48 fathoms on soft, green mud; 1092, off La Jolla in 40 fathoms on sand and shells.

***Halosydna insignis* Baird**

Lepidonotus insignis Baird (1863), p. 106.

Halosydna insignis, Baird (1865), p. 188.

Polynoe brevisetosa, Johnson (1897), p. 167, pl. 6, fig. 24; pl. 7, figs. 31, 40, 40a; pl. 8, figs. 46, 46a.

Halosydna insignis Moore (1910), p. 329.

Collected north of San Francisco from Kodiak Island, Alaska; Alki Point, Puget Sound; Trinidad; Cape Mendocino; Point Arena; Dillon's Beach; Tomales Bay; Duxbury Reef. Collected in San Francisco Bay from Fort Point, Point Cavallo, Lime Point, Black Point, Sausalito, San Antonio (Oakland) Creek, and Session's Basin. Collected south of San Francisco from Point San Pedro (11 miles south of Golden Gate); Pillar Point, California; Monterey; Pacific Grove; Avalon, Santa Catalina Island; La Jolla. Collected also in the following hauls: XVII, off San Pedro in 4 to 10 fathoms of fine sand; LXXXII-1, off Point Firmin in 27 to 30 fathoms on fine gray sand; 1166, off La Jolla in 5 to 13 fathoms on sand.

***Halosydna californica* Johnson**

Polynoe reticulata Johnson (1897), p. 170, pl. 7, figs. 32, 41, 41a; pl. 8, figs. 47, 47a, 47b.

Polynoe californica Johnson (1901), p. 387.

Collected from Humboldt Bay; Pacific Grove; Santa Barbara; Deadman's Island near San Pedro; Portuguese Bend; San Pedro; Avalon, Santa Catalina Island; La Jolla; Zuninga Point, Ballast Point, and Coronado in San Diego Bay. Collected also in the following hauls: XIII, off San Pedro in 35 to 36 fathoms on coarse sand; XIV-1, off San Pedro in 9 fathoms on small rocks; XVII-2, off San Pedro in 4 to 10 fathoms on fine sand; XLVII-2, off San Diego in 8 to 11 fathoms on hard sand and pebbles; LVI, in the mouth of San Diego Bay in 5 to 9 fathoms on sand and eel-grass; LVIII, off the Coronado Islands in 15 to 18 fathoms on sand and broken shells; LXII, off San Diego in 16 to 18 fathoms on fine gray sand; LXIII, off San Diego on a rocky bottom in 20 fathoms; LXIV, off San Diego on a sandy bottom in 11 to 19 fathoms; LXVII, off San Diego in 19

to 31 fathoms on grayish-yellow sand; LXXVIII, from the piles of the Santa Fé wharf in San Diego Bay; 4, off San Diego in a tow-net hauled from 65 fathoms to the surface; 5-6, off San Diego in a tow-net hauled from 90 fathoms to the surface; 1165, off La Jolla in 4 to 8 fathoms on sand.

***Halosydna carinata* Moore**

Halosydna carinata Moore (1903), p. 417, pl. 23, figs. 16-17.

Collected in haul L-1, off San Diego in 21 to 28 fathoms on rock. Other specimens, from an unknown locality, agreed with Moore's description except with respect to the structure of the notopodial setae. Dorsally there are a few of the forms described by Moore (1903), but ventrally there is a tuft of much longer delicate sharp-pointed setae, with comb-shaped teeth in two rows throughout the greater part of the seta, but not extending to the tip.

***Halosydna lordii* Baird**

Halosydna lordii Baird (1865), p. 190.

Polynoe lordii Johnson (1897), p. 175, pl. 7, figs. 35, 44; pl. 8, figs. 51 51a-b.

Collected from Yakutat, Alaska; Alki Point, Puget Sound; Anacortes, Wash.; Cape Mendocino; and San Pedro.

***Polynoe fragilis* Baird**

Lepidonotus fragilis Baird (1863), p. 108.

Halosydna fragilis Baird (1865), p. 191.

Polynoe fragilis Johnson (1897), p. 179, pl. 7, figs. 36, 45; pl. 8, figs. 52, 52a-b.

Collected from Pleasant Beach, Port Orchard, Salmon Bay, and Seattle, Wash.

The collection contained one bottle with a single specimen labeled *Polynoe commensalis*, but with no record of the identifier. It may have been identified as the species to which Webster (1879, p. 10) gave the name *Lepidametria commensalis*, but as it had lost all elytra and cirri, I was unable to be certain as to its position.

***Lepidonotus squamatus* Linnaeus**

Aphrodita squamata Linnaeus (1776), p. 1084.

Polynoe squamata Johnson (1897), p. 166, pl. 7, fig. 30.

Collected from Point Cavallo and Black Point in San Francisco Bay; Monterey Bay; and Santa Monica.

Lepidonotus robustus Moore

Lepidonotus robustus Moore (1905a), p. 544, pl. 36, figs. 32-35.

Locality unknown.

Lepidonotus coeloris Moore

Lepidonotus coeloris Moore (1903), p. 412, pl. 23, fig. 12.

Collected from Ballast Point, San Diego Bay, and in the following hauls: XVIII, off San Pedro in 17 to 33 fathoms on sand and mud; LXIX-2, off San Diego on a rocky bottom in 29 to 32 fathoms; LXXXII-1, off Point Firmin in 27 to 30 fathoms on fine gray sand; 1541, off San Clemente Island in 135 to 500 fathoms on gray mud; 1552, off San Clemente Island in 48 fathoms on coarse sand.

Harmothoe hirsuta Johnson

Harmothoe hirsuta Johnson (1897), p. 182, pl. 6, figs. 27-29; pl. 7, fig. 38; pl. 8, figs. 53, 53a-c.

Collected from Pillar Point, California; Pacific Grove; Santa Barbara; San Pedro Harbor; Portuguese Bend and White's Point near San Pedro; La Jolla; and San Diego Bay.

Harmothoe imbricata Linnaeus

Aphrodita imbricata Linnaeus (1788), p. 1084.

Harmothoe imbricata Malmgren (1865), p. 66.

Collected from Yakutat, Muir Inlet, and Kodiak Islands, Alaska; Alki Point, Puget Sound; Trinidad; Humboldt Bay; Shelter Cove, Mendocino County; Point Arena; Dillon's Beach; Tomales Bay; Fort Point and Point Cavallo, San Francisco Bay; Pacific Grove; La Jolla; and San Clemente Island. Collected also in the following hauls: XIII, off San Pedro on a sandy bottom in 35 to 36 fathoms; XLVII, off San Diego in 8 to 11 fathoms on hard sand and pebbles; LXVII, off San Diego in 19 to 31 fathoms on grayish-yellow sand.

Harmothoe crassicirrata Johnson

Harmothoe crassicirrata Johnson (1897), p. 183, pl. 6, figs. 25-26, pl. 7, fig. 39; pl. 8, figs. 54, 55a-c.

Collected from Monterey Bay.

Lepidasthenia gigas Johnson

Polynoe gigas Johnson (1897), p. 172, pl. 7, figs. 33, 42, 42a; pl. 8, figs. 48, 48a-b, 49.

Lepidasthenia gigas Moore (1909a), p. 241.

Collected from San Pedro; Point Loma, San Diego; and in haul LXXXIII, off Point Firmin in 60 to 140 fathoms on sand and broken shells.

Eunoa barbata Moore

Eunoa barbata Moore (1903), p. 334, pl. 28, figs. 1-6.

Collected from Blunt's Reef.

Family SIGALIONIDAE

Peisidice aspera Johnson

Peisidice aspera Johnson (1897), p. 184, pl. 9, figs. 56-59;; pl. 10, figs. 63a-d.

Collected from Dillon's Beach; Monterey Beach; and San Diego.

Sigalion pourtalesii Ehlers

Sigalion pourtalesii Ehlers (1887), p. 57, pl. 15, figs. 1-4; pl. 16, figs. 1-10.

These differed from Ehler's description only in that each had a small median tentacle near the posterior part of the head.

Collected from San Pedro; Ballast Point, San Diego Bay; also in the following hauls: VI-2, off San Pedro in 14 to 20 fathoms on gray sand; XIV-3, off San Pedro in 40 to 150 fathoms on gray mud; LXXIII-2, off San Diego in 59 to 106 fathoms on green mud and sand.

Sthenelais tertiaglabra Moore

Sthenelais tertiaglabra Moore (1910), p. 395, pl. 33, figs. 113-120.

Locality unknown.

Sthenelais fusca Johnson

Sthenelais fusca Johnson (1897), p. 185, pl. 9, figs. 60, 61, 61a, b; pl. 10, figs. 64, 64a-g.

The appearance of preserved specimens varied with the preservative used. Specimens in alcohol had brick-red elytra, while those in formalin were anteriorly quite transparent, with yellowish pigment granules toward the posterior end.

Collected from San Pedro and also in the following hauls: VIII, along shore in the mud near the Southern Pacific Railroad bridge in the inner San Pedro Harbor; XLIII-1, in San Diego Bay in 3 to 7 fathoms on soft black mud; LXXIX-1, off San Diego in 63 to 65 fathoms on green mud and broken shells.

***Sthenelais verruculosa* Johnson**

Sthenelais verruculosa Johnson (1897); p. 187, pl. 9, figs. 62, 62a; pl. 10, figs. 65, 65a-d.

Collected off White's Point, San Pedro (type specimen); and San Diego.

***Sthenelanelle uniformis* Moore**

Sthenelanelle uniformis Moore (1910), p. 391, pl. 33, figs. 105-112.

These showed on posterior somites a tuft of long delicate capillary setae arising from the neuropodium, a structure not mentioned in Moore's description.

Collected in haul X, off San Pedro in 19 to 38 fathoms on green mud.

***Panthalis pacifica* sp. nov.**

Pl. 11, figs. 1-7

The head (pl. 11, fig. 1) has its greatest transverse diameter about equal to its antero-posterior diameter measured to the base of the ommatophores. Its basal portion is rather narrow, swelling abruptly on either side and then gradually narrowing to the bases of the ommatophores. These are provided with very large eyes, which occupy more than half their length, while a second pair of much smaller eyes lies just posterior to the bases of the ommatophores. The head is divided longitudinally by a shallow median groove and, at about its center, a median tentacle arises from a very short ceratophore. The median tentacle is rather slender and gradually tapers to an acute tip, its apex extending beyond the eyes. The ventral tentacles, like the median one in size and form, arise close together on the ventral surface of the head. The palps are long and each tapers uniformly to an acute tip. The tentacular cirri are larger than the antennae. While, in preserved material, the surface of the head is light brown in color, all its appendages are colorless.

All elytra are very delicate, with entire margins. The anterior two or three pairs cover the entire dorsal surface of the body. Then,

back to about the twenty-fifth somite, there is a wider uncovered area; this area narrows, at this somite, to less than the width of an elytron and maintains this width to the posterior end. No specimen was entire, the longest fragment having about twenty-five elytra. They are on somites 2, 4, 5, 7, 9, etc., and are more or less pigmented. When the pigment is small in amount it is collected near the elyrophore and spreads from this towards the margin. In one specimen the elytra were almost entirely dark brown, and in some others there was an indication of a median dorsal longitudinal pigmented band on the body wall.

The protruded proboscis is as long as the first twenty somites. On the mid-dorsal line at the apex of the proboscis is a rigid cirrus-like process about equal to a palp in size. A much smaller process is opposite it on the mid-ventral line. Between these two processes the soft margin of the proboscis has about twelve lobes on either side, the apex of each lobe being truncated and having a black pigment spot on its outer surface. Above and below, on either side of the mid-line, is a long, light-brown tooth, with rows of smaller teeth running laterally from it.

The first parapodium (pl. 11, fig. 2) is narrow and elongated, with its presetal lobe longer and narrower than its postsetal one. The postsetal lobe is in two parts, of which the dorsal is the larger. Its ventral portion is apparently continuous with a short cirrus-like lobe which lies in front of it. A spreading tuft of setae comes out between these lobes. Each dorsal seta has a long, smooth base, which suddenly widens at about its middle and then gradually narrows to an acute point. All of the terminal portion of each is armed along one edge with several rows of very sharp spines (pl. 11, fig. 4). The setae at the ventral edge of the tuft are smaller and not so numerous as the others, but are similar to them in form. An aciculum extends into the base of the elyrophore, and another extends into the parapodium. The ventral cirrus is very long.

The subsequent parapodia (pl. 11, fig. 3 of the 8th) are larger and relatively broader than the first, and the ventral cirri become slightly smaller absolutely, and much smaller relatively, than on the first. There are two sorts of setae on these parapodia. Ventrally there is a tuft of sickle-shaped setae (pl. 11, fig. 5), each of which has its central axis longitudinally striated at the bend, where a series of relatively large spines begins. Toward the end of each seta these large spines are replaced by several rows of much smaller ones. The details

of their arrangement are hard to make out, and their appearance varies with the position of the seta. Apparently there are several rows so arranged as to give a double-bordered effect for the greater part of the terminal portion of the seta. Just beyond the bend are a number of very fine spines arranged in transverse rows. Dorsal to these is a vertical row of very stout setae which extend beyond the parapodium to a distance equal to about half the length of the latter. These setae are light brown and the apex of each is prolonged into a long spine with a diminishing series of smaller spines arising from it (pl. 11, fig. 6). The whole terminal portion of each seta is covered with minute spines. Appearing as early as the eighth somite there is a tuft of three or four setae located dorsally to the large ones. Each has a smooth basal portion, narrowed to a symmetrically pointed apex, from either side of which a tuft of fibres is given off which form an irregular fan-like arrangement (pl. 11, fig. 7). These setae are much smaller than the heavy ones and extend only about half as far beyond the parapodium.

Type specimen collected in haul 1497, off San Diego ($32^{\circ} 50'7''$ N and $117^{\circ} 21'5''$ W) in 50 to 100 fathoms on black sand. Others collected in the following hauls: XII-2, off San Pedro in 35 to 175 fathoms on black asphalt rocks, pebbles, coarse sand, and broken shells; XIV-3, off San Pedro in 40 to 150 fathoms on gray mud; XXI-5, off Santa Catalina Island in 150 fathoms; LXX-6, off La Jolla in 54 to 125 fathoms on mud, sand, and rock; LXXII-3, off San Diego in 45 to 50 fathoms on foul, dark green mud; LXXIII-3, off San Diego in 57 to 106 fathoms on dark green mud and fine sand; LXXIX-1, off San Diego in 63 to 65 fathoms on green mud and broken shells; 1145, inside the kelp near La Jolla in 30 fathoms on sandy mud; 1475, off La Jolla in 50 to 100 fathoms on fine sand.

Type specimen in Museum of the University of California; co-type in American Museum of Natural History.

Family PHYLLODOCIDAE

Phyllodoce ferruginea Moore

Phyllodoce ferruginea Moore (1909b), p. 337, pl. 15, figs. 15-18.

Collected from Pacific Grove; Avalon, Santa Catalina Island; also in haul III, off San Pedro in 7 fathoms on dark brown mud.

Phyllodoce castanea v. Marenzeller

Phyllodoce castanea v. Marenzeller (1897), p. 127, pl. 3, fig. 2.

Phyllodoce castanea Moore (1909a), p. 239.

Collected from Cape Mendocino; San Pedro; also in haul XXVI, off Santa Catalina Island in 46 to 49 fathoms on sand.

Phyllodoce medipapillata Moore

Phyllodoce medipapillata Moore (1909a), p. 237, pl. 7, figs. 3-4.

While agreeing in all essential respects with Moore's descriptions, these showed a considerable amount of variation. The papillae at the end of the proboscis vary in number from 17 to 19 and the head may vary in form, being in some cases as broad as it is long, while in others the length is less than the breadth. The pygidium had been lost in Moore's specimens. Some in this collection had two very stout anal cirri, tapering at the end to a sharp point.

Collected from Bolinas Cove; Pillar Point, California; San Pedro; Avalon, Santa Catalina Island; La Jolla; and Point Loma, San Diego Bay. Collected also in the following hauls: XIV-2, off San Pedro in 24 to 240 fathoms on greenish-brown mud and fine gray sand; XXVIII-1, off Santa Catalina Island in 12 to 30 fathoms on coarse sand and broken shells; L-1, off San Diego on a rocky bottom in 21 to 28 fathoms; LXII, off San Diego in 16 to 18 fathoms on gray sand; LXX-5, off La Jolla in 54 to 118 fathoms on mud and adobe shale rock; LXXXII-1, off Point Firmin in 27 to 30 fathoms on fine gray sand.

Eulalia quinquelineata Treadwell

Eulalia quinquelineata Treadwell (1900), p. 192, figs. 27-29.

Locality unknown.

Eulalia longicornuta Moore

Eulalia longicornuta Moore (1906), p. 222, pl. 10, figs. 7-8.

Collected from Pacific Grove.

Eulalia bifoliata Moore

Eulalia bifoliata Moore (1909b), p. 349, pl. 16, figs. 31-34.

Collected in haul 1555, off San Clemente Island in 50 fathoms on coarse sand.

Eulalia sp. (?)

Collected from Black Point, San Francisco Bay.

Notophyllum imbricatum Moore

Notophyllum imbricatum Moore (1906), p. 217, pl. 10, figs. 1-3.

Collected from Portuguese Bend (near San Pedro), and San Diego.

Family TOMOPTERIDAE**Tomopteris septentrionalis Apstein**

Tomopteris septentrionalis Apstein (1900), p. 41, pl. 12, figs. 16-17.

Collected in the following hauls: 1680 and 1719, surface tows off La Jolla; 1729, 250 fathom tow made off La Jolla with a Kofoid closing-net; 1769, surface tow off San Clemente Island; 1813, 100 fathom tow made off La Jolla with a Kofoid closing-net; 1848, 75 fathom tow made off La Jolla with an open tow-net.

Family NEREIDAE**Nereis vexillosa Grube**

Nereis vexillosa Grube (1851), p. 4, pl. 2, figs. 1, 5, 6.

Nereis vexillosa Ehlers (1864), p. 573, pl. 23, figs. 3-5.

The animals of this species have in the posterior somites the peculiar pointed setae noted by Johnson (1901, p. 400) as characteristic of *Nereis procera*. On this account it is easy to mistake the young of *N. vexillosa* for *N. procera*, as the form of the head and tentacles vary with the method of preservation.

Collected from Aleutian Islands, Ocean Cape, Yakutat, Prince William Sound, and Kodiak Islands in Alaska; Baker's Beach and Beaver Cove near Vancouver; Orcas Island, Port Orchard, and Alki Point in Puget Sound; Trinidad; Point Arena; Point Reyes; Dillon's Beach; Bolinas; Duxbury Reef; Fort Point, San Antonio Creek, West Berkeley, Session's Basin, and Land's End in San Francisco Bay; Point San Pedro; Pacific Grove; Santa Barbara; Avalon, Santa Catalina Island; La Jolla; and San Diego. Collected also in the following hauls: XXVIII-2, off Santa Catalina Island in 15 to 45 fathoms on coarse sand and broken shells; LVIII, off the Coronado Islands in 15 to 18 fathoms on sand and broken shells; LIX, off the Coronado Islands in 15 fathoms on fine gray sand; LXXVII, in San Diego Bay in 3 fathoms on hard sand and rock.

Nereis procera* EhlersNereis procera* Ehlers (1864), p. 557, pl. 23, fig. 2.

Collected from Kodiak Islands and Yakutat, Alaska; Pleasant Beach, Puget Sound; Black Point, San Francisco Bay; Pacific Grove; Portuguese Bend; Avalon, Santa Catalina Island; and San Diego. Collected also in the following hauls: XV, off San Pedro in 4 to 7 fathoms on coarse sand; XVI-2, off San Pedro in 9 fathoms on small rocks; XVII, off San Pedro in 4 to 10 fathoms on fine sand; XIX-2, off San Pedro in 30 to 77 fathoms on soft sandy mud with many pebbles; XLII, in San Diego Bay in 3 to 7 fathoms on soft black mud; XLIII-1, in San Diego Bay in 3 to 7 fathoms on soft black mud; XLVII-2, off San Diego in 8 to 11 fathoms on hard sand and pebbles; 1551, off San Clemente Island in 48 fathoms on coarse sand.

Nereis agassizi* EhlersNereis agassizi* Ehlers (1864), p. 542, pl. 23, fig. 1.

This species is numerous and occurs with *Nereis procera*. The two species are similar, but *N. agassizi* has a peculiar hooked seta in the posterior somite, while *N. procera* has, in this region, a peculiar seta whose terminal joint fits into a socket at the end of the basal. *N. agassizi* has in the fifth and immediately following somites, a peculiar swelling on the parapodium. The characters of the head, antennae, etc., vary with the mode and degree of preservation.

Collected from Port Orchard and Channel Rocks in Puget Sound; Trinidad; Humboldt Bay; Cape Mendocino; Duxbury Reef; Fort Point, Lime Point, and Black Point in San Francisco Bay; Pacific Grove; Santa Barbara; San Pedro; Avalon, Santa Catalina Island; San Diego Bay; San Clemente Island; and Honolulu Harbor. Collected also in the following hauls: II-2, in San Pedro Harbor in 2 to 3 fathoms on quantities of sea-weed; VI-2, in the outer San Pedro Harbor in 3 fathoms on gray sand; XV, off San Pedro in 4 to 7 rocks; XVI-2, off San Pedro in 17 fathoms on pebbles and small rocks; XVII, off San Pedro in 4 to 10 fathoms on fine sand; XXVIII-1, off Santa Catalina Island in 12 to 30 fathoms on coarse sand and broken shells; XLIII-2, and 3, in San Diego Bay in 5 to 8 fathoms on soft black mud; XLVI-1 and 2, in San Diego Bay on a sandy bottom in 5 fathoms; XLVII-1 and 2, off San Diego in 8 to 10 fathoms on hard sand; LIX, off the Coronado Islands in 15 fathoms

on fine gray sand; LXII, off San Diego in 16 to 18 fathoms on gray sand; LXIV, off San Diego on a sandy bottom in 11 to 19 fathoms; LXVII, off San Diego in 19 to 31 fathoms on grayish-yellow sand; LXXI, off La Jolla in 15 to 56 fathoms on soft mud; LXXXI-2, off San Diego in 15 to 25 fathoms on sand and rock; LXXXII-2, off Point Firmin in 30 fathoms; 1165, off La Jolla in 4 to 8 fathoms on sand; 1556, off San Clemente Island in 50 fathoms on black mud and coarse sand; 1561, on Cortez Banks in 11 to 16 fathoms on rocks; 1630-31, near Guadalupe Island off the coast of Lower California in 18 fathoms on broken shells; 1632, near Guadalupe Island in 40 fathoms on green mud.

***Nereis cyclurus* Harrington**

Nereis cyclurus Harrington (1897), p. 214, pls. 16-18.

Collected from Pacific Grove; and Point Loma, San Diego.

***Nereis virens* var. *brandti* Malmgren**

Alitta brandti Malmgren (1865), p. 183.

Collected from Pleasant Beach, Puget Sound; Bolinas Bay; and San Pedro.

***Nereis virens* Sars**

Nereis virens Sars (1835), p. 58, pl. 10, fig. 27.

Nereis virens Ehlers (1864), p. 559, pl. 22, figs. 29-32.

Collected from San Pedro.

***Nereis virens* var. *plenidentata* Moore**

Nereis virens var. *plenidentata* Moore (1909a), p. 244.

Collected in tide pools at Deadman's Island, San Pedro.

***Nereis tentaculata* Kinberg**

Nereis tentaculata Kinberg (1865), p. 170.

Collected from Pacific Grove.

***Nereis paucidentata* Moore**

Nereis paucidentata Moore (1903), p. 430, pl. 23, figs. 28-30.

Collected from Avalon, Santa Catalina Island.

***Nereis notomacula* sp. nov.**

Pl. 11, figs. 8-12

The prostomium is bluntly rounded anteriorly, its anterior third being roughly rectangular in outline and its posterior two-thirds rounded (pl. 11, fig. 8). The eyes were not clearly seen, their position being indicated merely by a pair of swellings on either side of the head. The antennae are about as long as the head and gently taper to their apices. The tentacular cirri are unequal in length, the dorsal ones reaching to the eighth setigerous somite while the ventral ones are much shorter. Each has a prominent basal piece and a long tapering terminal joint. The basal part of the jaw is black and the terminal portion is translucent brown. The jaw has eight to ten teeth along its concave edge. There is an oval area of paragnaths near the base of the jaw with eight vertical rows of paragnaths just below it. The head, body, and basal joint of each cirrus are dark brown, while the terminal parts of the cirri and palps are colorless. At the end of the basal joint of each palp is a band of dark-brown spots. Near the apex of the prostomium are a median and two lateral dark patches of pigment with a line extending from each lateral patch nearly to the posterior border of the head. Just behind the anterior border of each somite is a transverse row of dark spots which, throughout the posterior part of the body, terminates in a prominent black spot just dorsal to the parapodium. The first four parapodia show much black pigment in both rami while in the next nine or ten, pigment is present only in the basal portion of the dorsal cirrus. Throughout the posterior part of the body the pigment is arranged in prominent patches, one dorsal and one ventral to the parapodium on the body wall, one on the basal part of the dorsal cirrus, two in the notopodium, and one in the neuropodium.

The first parapodium (pl. 11, fig. 9) has single dorsal and ventral lobes, and narrow postsetal ones. There is a single dense tuft of compound setae of the usual *Nereis* type with rather large terminal joints. The dorsal cirrus extends for more than half its length beyond the parapodium, while the ventral cirrus is hardly longer than the parapodium.

Of the *subsequent parapodia* (pl. 11, fig. 10 of the 8th) those from the fifth to the thirteenth are very thick and fleshy. There are two equal postsetal notopodial lobes, and one large and one very small postsetal neuropodial lobe. In addition, there is an incon-

spicuous presetal cirrus-like lobe. As in the first parapodium, the dorsal cirrus extends for more than half its length beyond the parapodium, while the ventral cirrus is much smaller than that in the first parapodium. The greater number of neuropodial setae each have a short terminal joint provided with a strong apical tooth and a row of sharp spines along one edge (pl. 11, fig. 11), while a few, dorsally located, resemble the notopodial setae in form.

In the type, beginning at about the end of the anterior quarter of the body, each notopodium has a few hooked setae (pl. 11, fig. 12). The posterior parapodial lobes are much more slender than the anterior ones. The anal cirri were absent from the type, but present in a fragment in the same bottle. They are longer than the tentacular cirri, and very slender. On the body wall, at the base of each cirrus, is a very prominent black spot.

Collected from Fort Point, San Francisco Bay.

Type in the Museum of the University of California; co-type in the American Museum of Natural History.

Family NEPHTHYDIDAE

I have attempted to distinguish between the species in this collection, though it is probable that Moore (1911, p. 243) is correct in thinking that all of the California species belong to *Nephtys coeca*.

Nephtys malmgreni Theel

Nephtys longisetosa Malmgren (1865), p. 106, pl. 12, fig. 20.

Nephtys malmgreni Theel (1879), p. 26.

Collected from San Pedro; Point Loma, Ballast Point, Middle Ground, and La Playa in San Diego Bay; also in the following hauls: XLI-1 to 5, in San Diego Bay in 2 to 3 fathoms on coarse sand and broken shells; LXXVI, in San Diego Bay in 2 to 3 fathoms on coarse yellow sand and broken shells; 1632, near Guadalupe Island in 40 fathoms on green mud.

Nephtys coeca Fabricius

Nereis coeca Fabricius (1799), p. 185, pl. 4, figs. 24-29.

Nephtys coeca Oersted (1843a), p. 41, figs. 73-74, 77, 79-86.

Nephtys coeca Malmgren (1865), p. 104, pl. 12, figs. 18-18c.

Collected from Popoff Islands, Alaska; Pleasant Beach, Puget Sound; and Humboldt Bay.

Nephtys assimilis* OerstedNephtys assimilis* Oersted (1843b), p. 33, figs. 93, 100.*Nephtys assimilis* Malmgren (1865), p. 105.

Collected from West Berkeley; Santa Barbara; San Pedro; and Point Loma and Ballast Point in San Diego Bay. Collected also in the following hauls: VI-2, in the outer San Pedro Harbor in 3 fathoms on gray sand; XIII, off San Pedro in 35 to 36 fathoms on sand; LII, in the sand and mud along the shore of San Diego Bay; LXXIII-3, off San Diego in 57 to 106 fathoms on dark-green mud and sand; LXXV, off National City in San Diego Bay on a muddy bottom in 2 to 3 fathoms; LXXIX-1, off San Diego in 63 to 65 fathoms on green mud and broken shells.

Nephtys incisa* MalmgrenNephtys incisa* Malmgren (1865), p. 105, pl. 12, figs. 21-21c.

Collected in haul 1165, off La Jolla in 4 to 8 fathoms on soft black shale.

Family LEODICIDAE

In accordance with the rule of priority, *Eunice* should be replaced by *Leodice* for a generic annelidan term, *Eunice* having been in use for insects prior to its use by Cuvier for annelids. Accordingly *Leodice* will be used in the following descriptions.

Leodice kobiensis* McIntoshEunice kobiensis* McIntosh (1885), p. 278, pl. 38, figs. 12-13; pl. 20a, figs. 1-3.

A single specimen, probably of this species, was collected from Pacific Grove.

Leodice biannulata* MooreEunice biannulata* Moore (1904), p. 484.

Moore states that the nuchal cirri resemble the tentacles. In these specimens they often resemble the dorsal cirri by having no more than three joints. The ventral crochet and aciculum of the middle region of the body are as in figure 13, plate 11, thus not agreeing exactly with Moore's description. These differences, however, do not seem to me to be of specific importance.

Collected from Cape Mendocino; Pacific Grove; White's Point, near San Pedro; and La Jolla. Collected also in the following hauls: II-1, in San Pedro Harbor in 2 fathoms on quantities of sea-weed; XXI-2, off Santa Catalina Island in 43 to 77 fathoms on pebbles and stones; LIX, off the Coronado Islands in 15 fathoms on fine gray sand; LXX-7, off La Jolla in 55 to 125 fathoms on soft black shale; 1155, off La Jolla in 70 fathoms on green mud.

***Leodice hawaiiensis* Treadwell**

Eunice hawaiiensis Treadwell (1906), p. 1166.

Collected in the following hauls: XII-2, off San Pedro in 35 to 175 fathoms on black asphalt rocks, pebbles, coarse sand, and broken shells; XVIII, off San Pedro in 17 to 33 fathoms on sandy mud; LXX-2, off La Jolla in 54 to 98 fathoms on soft black shale; L-5, off La Jolla in 54 to 118 fathoms on mud and soft black shale; LXXX-1, off San Diego in 135 fathoms on greenish-gray mud and sand; 1124, off La Jolla in 160 fathoms on green mud; 1145, off La Jolla in 30 fathoms on sand and mud; 1157, off La Jolla in 160 fathoms on green mud.

***Marphysa californica* Moore**

Marphysa californica Moore (1909a), p. 251, pls. 7-8, figs. 13-20.

Moore did not describe the pygidium which was present on some of these forms. Anus dorsally directed, with swollen lips. Two pairs of anal cirri, the dorsal pair being enlarged for about one-third of their length and then, narrowing suddenly, gradually tapering toward their ends. Ventral pair much smaller.

Collected from White's Point, near San Pedro; San Diego; Coronado; and Kakaako Reef, Oahu. Collected also in haul LII, in the mud and sand along the shore of San Diego Bay.

***Marphysa stylobranchiata* Moore**

Marphysa stylobranchiata Moore (1909a), p. 249, pl. 7, figs. 8-12.

Apparently the character of the prostomium in this species is subject to considerable variation. The length may be equal to the width, and the groove dividing it into two rings may not be present. Some gills, apparently as an exception, show a bifid character.

Collected from Black Point, San Francisco Bay; Pillar Point, California; Pacific Grove; Deadman's Island, San Pedro; and Coronado.

Hyalinoecia tubicola* O. F. MüllerNereis tubicola* Müller (1787), p. 18, pl. 18, figs. 1-6.*Hyalinoecia tubicola* Malmgren (1867), p. 181, pl. 9, fig. 49.

Collected in the following hauls: V-1, off San Pedro in 10 to 24 fathoms on gray sand and mud; X, off San Pedro in 19 to 38 fathoms on green mud; XII-2, off San Pedro in 35 to 175 fathoms on black asphalt rocks, pebbles, coarse sand, and broken shells; XIII, off San Pedro in 35 to 36 fathoms on coarse sand; XVIII, off San Pedro in 17 to 33 fathoms on sandy mud; XIX-4, off San Pedro in 30 to 75 fathoms on soft mud, coarse sand, and pebbles; LXXIX-1, off San Diego in 63 to 65 fathoms on green mud and broken shells.

Diopatra californica* MooreDiopatra californica* Moore (1904), p. 484, pl. 37, figs. 1-9.

These differed from Moore's description in that the dorsal cirri of the first somite were always larger, instead of smaller, than the ventral cirri.

Collected from Pacific Grove; Santa Barbara; White's Point, San Pedro; San Diego; and Coronado. Collected also in the following hauls: XIV-1, off San Pedro in 40 to 155 fathoms on soft sticky mud; XIX-1, off San Pedro in 30 to 100 fathoms on soft mud, sand, and pebbles; XLV, about the rocky shore of San Diego Bay; LII, in the mud and sand along the shore of San Diego Bay; 1112, off La Jolla in 45 fathoms on green mud and fine sand; 1632, near Guadalupe Island in 40 fathoms on green mud.

Northia geophiliformis* MooreNorthia geophiliformis* Moore (1903), p. 445.

Collected from Bolinas Point; Pacific Grove; and in haul VI-1, in the outer San Pedro Harbor in 3 fathoms on gray sand.

Northia elegans* JohnsonNorthia elegans* Johnson (1901), p. 406, pl. 8, figs. 77-85.

Collected from Neah Bay, Washington.

Onuphis parva* MooreOnuphis parva* Moore (1911), p. 263, pl. 17, figs. 51-57; pl. 18, figs. 98-99.

Locality unknown.

Arabella attenuata Treadwell

Arabella attenuata Treadwell (1906), p. 1172, fig. 62.

Collected from Patrick's Point, California; Pacific Grove; San Pedro; Santa Catalina Island; San Clemente Island; and in haul XLV, along the rocky shore of San Diego Bay.

Lumbrinereis bifurcata McIntosh

Lumbriconereis bifurcata McIntosh (1885), p. 241, pl. 36, figs. 10-12; pl. 17a, fig. 16.

Collected in haul X, off San Pedro in 19 to 38 fathoms on mud; and in haul 1102, off La Jolla in 15 to 35 fathoms on sand, mud, and broken shells.

Lumbrinereis zonata Johnson

Lumbriconereis zonata Johnson (1901), p. 408, pl. 9, figs. 93-100.

Collected from Tomales Bay; Bolinas Point; Pillar Point, California; Pacific Grove; Moss Beach, Monterey Bay; Santa Barbara; and San Pedro. Collected also in the following hauls; X, off San Pedro in 19 to 38 fathoms on mud; XIV-2, off San Pedro in 25 to 240 fathoms on greenish-brown mud and gray sand; XXXVI-3, off Santa Catalina Island in 60 to 125 fathoms on green mud and sand; LXXII-3, off San Diego in 45 to 50 fathoms on foul, dark-green mud; LXXIV, in San Diego Bay in 1.5 to 2 fathoms on mud and broken shells; LXXXII-1, off Point Firmin in 27 to 30 fathoms on fine gray sand; 1145, off La Jolla in 30 fathoms on sand and mud.

Lumbrinereis erecta Moore

Lumbrinereis erecta Moore (1904), p. 490, pl. 37, figs. 19-22; pl. 38, figs. 23-25.

Following Moore's description I have listed as *Lumbrinereis erecta* all specimens whose heads agreed with the type in structure, and that at the same time showed an unusual development of the dorsal parapodial lobe. In this latter respect there is very great variation. Some specimens have these lobes so large as to overlap the dorsal surface of the body. In others, especially those killed in corrosive, they are much smaller.

Collected from Bolinas Bay; Black Point, San Francisco Bay; Pacific Grove; Santa Barbara; Deadman's Island, San Pedro; La Jolla; San Diego; and Coronado. Collected also in the following

hauls: VI-2, in the outer San Pedro Harbor in 3 fathoms on gray sand; XII-2, off San Pedro in 35 to 175 fathoms on black asphalt rocks, pebbles, coarse sand, and broken shells; XLIII-2, in San Diego Bay in 5 to 8 fathoms on soft black mud; LXX-5, off La Jolla in 54 to 118 fathoms on green mud and soft black shale; LXXV, in San Diego Bay on a muddy bottom in 2 to 3 fathoms; LXXVIII, from the piles of the Santa Fé wharf in San Diego Bay.

***Stauronereis moniloceros* Moore**

Stauronereis moniloceros Moore (1909a), p. 256, pl. 8, figs. 24-29.

Collected from Point Pinos; and Pacific Grove.

***Ninoe palmata* Moore**

Ninoe palmata Moore (1903), p. 456, pl. 26, figs. 68-71.

Collected in haul 1112, off La Jolla in 45 fathoms on green mud and fine sand; also one specimen from an unknown locality.

Family GLYCERIDAE

***Glycera rugosa* Johnson**

Glycera rugosa Johnson (1901), p. 409, pl. 10, figs. 101-102.

Collected from Pleasant Beach, Puget Sound; Tomales Bay; San Pedro; and Point Loma, Zuinga Point, and Coronado in San Diego Bay. Collected also in the following hauls: XXXVI-3, off Santa Catalina Island in 60 to 125 fathoms on green mud and sand; XLI-4 and 5, in San Diego Bay in 2 to 3 fathoms on sand and broken shells; XLIII-1, in San Diego Bay in 3 to 7 fathoms on soft black mud; XLIII-2 and 3, in San Diego Bay in 5 to 8 fathoms on foul black mud; LII, in the mud and sand along the shore of San Diego Bay; LXXIV, in San Diego Bay in 1 to 2 fathoms on mud and broken shells; LXXV, in San Diego Bay on a muddy bottom in 2 to 3 fathoms; 1145, off La Jolla in 30 fathoms on sand and mud.

***Glycera nana* Johnson**

Glycera nana Johnson (1901), p. 411, pl. 10, figs. 103-103a.

Collected from Salmon Bay and Port Orchard in Puget Sound; San Clemente Island; and in the following hauls: 1112, off La Jolla in 45 fathoms on green mud and fine sand; 1541, off San Clemente Island in 136 to 500 fathoms on green mud.

Glycera alba Rathke

Glycera alba Rathke (1843), p. 173, pl. 9, fig. 9.

Glycera alba Ehlers (1864), p. 660.

Collected from San Pedro.

Glycera longipinnis Grube

Glycera longipinnis Grube (1878), p. 182, pl. 8, fig. 9.

Collected from San Pedro.

Glycera sp.(?) juv.(?)

Collected in haul LXXVI-2, in San Diego Bay in 2 to 3 fathoms on coarse yellow sand and broken shells.

Glycera capitata Oersted

Glycera capitata Oersted (1843b), p. 44, pl. 7, figs. 87-88.

Glycera capitata Ehlers (1864), p. 648, pl. 23, figs. 47-49.

Collected from Kodiak Islands and Orca in Prince William Sound, Alaska.

Goniada brunnea Treadwell

Goniada brunnea Treadwell (1906), p. 1174, figs. 68-70.

Collected from Deadman's Island near San Pedro, and also in haul 1112, off La Jolla in 45 fathoms on green mud and fine sand.

Goniada annulata Moore

Goniada annulata Moore (1905a), p. 549, pl. 36, figs. 45-48.

Collected in the following hauls: LXX-6, off La Jolla in 54 to 118 fathoms on mud, sand, and adobe shale rock; LXXI, off La Jolla in 15 to 57 fathoms on mud; LXXIII-3, off San Diego in 57 to 97 fathoms on dark green mud and sand; 1112, off La Jolla in 45 fathoms on green mud and sand; 1122, off La Jolla in 100 fathoms on green mud and sand.

Hemipodia borealis Johnson

Hemipodia borealis Johnson (1901), p. 411, pl. 10, figs. 104-104a.

Collected from Puget Sound; Trinidad; Tomales Bay; Bolinas Bay; San Pedro; San Diego; and in haul XLV, along the rocky shore of San Diego Bay.

Family ARICIIDAE

***Nainereis longa* Moore**

Nainereis longa Moore (1909a), p. 264.

In his description Moore does not mention minute denticulations which appear on the curved neuropodial spines.

Collected from Neah Bay, Alaska; Bolinas Bay; Black Point, San Francisco Bay; Pacific Grove; and Point Loma, San Diego.

***Nainereis robusta* Moore**

Nainereis robusta Moore (1909a), p. 262, pl. 8, figs. 34-37.

These, which agreed in other respects with Moore's descriptions, have the second somite continued forward to the posterior edge of the mouth, thus dividing the "posterior ring" of the peristomium into two parts.

Collected from Black Point, San Francisco Bay; and Pacific Grove.

***Scoloplos elongata* Johnson**

Scoloplos elongata Johnson (1901), p. 412, pl. 10, figs. 105-110.

Collected from Salmon Bay and Port Orchard, Puget Sound; Tomales Bay (entrance); and Coronado.

***Aricideopsis megalops* Johnson**

Aricideopsis megalops Johnson (1901), p. 413, pl. 10, figs. 111-112; pl. 11, figs. 113-114.

Locality unknown.

***Aricia* sp. (?)**

Collected from San Diego, Coronado, and also in haul XLIII-1, in San Diego Bay in 3 to 7 fathoms on soft black mud.

Family SPIONIDAE

***Spio acuta* sp. nov.**

Pl. 11, figs. 14-20

This species is represented in the collection by two specimens, both of which had lost their posterior ends. The length of the remaining portion is twenty millimeters, and the width one and one-half millimeters. The head (pl. 11, fig. 14) has a very acute prostomium. The

peristomium is relatively long and has a median dorsal elevation which appears like a posterior continuation of the prostomium, and is then itself continued into the base of a conical elevation on the dorsal surface of the first setigerous somite, the general effect being that of a median caruncle extending from the apex of the prostomium to the posterior border of the first setigerous somite (pl. 11, fig. 14). On either side an elevated ridge starts from the anterior face of the peristomium and extends, as a low wing, to the posterior edge of the somite. The tentacles are about four times longer than the head and arise from the posterior end of a depression bounded by the "wing" and the "caruncle." Each tentacle tapers regularly to its apex, with a faint groove on its dorsal surface. There are four small black eyes, the posterior ones being nearer together and a little larger than the anterior ones.

The first setigerous somite has a distinct neuropodium and notopodium, the setigerous lobe of the latter being more prominent than that of the former. Each has a prominent postsetal lobe, that of the notopodium being the larger (pl. 11, fig. 15).

On the second setigerous somite the neuropodial lobe is much longer and has, on one side, a broad wing which forms the gill. On the fifth and sixth somites the neuropodial lobes nearly meet on the mid-dorsal line. Farther back they retain this size though, with increasing width of body, more of the dorsal surface is left uncovered in the mid-line.

When fully developed the parapodium (pl. 11, fig. 16 of the 13th) shows prominent postsetal lobes, but the setae themselves arise directly from the body wall, without any definite setal lobe. The postsetal neuropodial lobe is rounded but not very prominent. The postsetal lobe of the notopodium is drawn out to form a prominent gill composed of a cirrus-shaped ciliated dorsal portion, which contains a blood-vessel in the form of a single loop, and a shorter, flattened ventral portion.

Behind the twenty-fifth somite the neuropodium and notopodium are widely separated so that the former is distinctly ventral and the latter distinctly dorsal. Between them the body-wall is much swollen (glandular?). A low vertical ridge unites the two parts of the parapodium. The gill has a dorsal keel as in the anterior somites, but it is smaller (pl. 11, fig. 18).

The setae of the first setigerous somite are relatively very long and longitudinally striated. Each gently tapers to its apex and has

a small wing along its middle half. Farther back these setae (pl. 11, fig. 17 of the 13th somite) are much stouter and their free portions are scarcely longer than the postsetal lobes. Each has a slight lateral expansion at the point where it leaves the body wall, and tapers from this point to an acute tip. The setae have prominent longitudinal striations. Those in the two lobes of the parapodium are similar, except that the most dorsally placed ones are a trifle longer.

There are only a few ventral setae. In the parapodium figured there were two sharp-pointed setae on its ventral side, each with a subterminal wing (pl. 11, fig. 19), and one, essentially similar in form, on its dorsal side. Between them are three hooded crochets, having obscure terminal teeth covered by a transparent hood (pl. 11, fig. 20). The dorsal setae, which are similar to those of the anterior somites, are longer and more numerous than the ventral ones.

Dorsally, a conspicuous white ridge crosses the middle of each somite.

Collected from San Diego.

Type in the Museum of the University of California; co-type in the American Museum of Natural History.

***Scolecopsis alaskensis* sp. nov.**

Pl. 12, figs. 21, 22

No specimen was entire. In the type, a fragment of the anterior end measured eighty millimeters for the first 130 somites. The width of the head, at its base, was five, and that of the second somite, eight millimeters. From here the width gradually increased to thirteen millimeters at the one hundred and thirtieth somite. Another specimen was considerably larger than the type.

The head is roughly triangular in form and is divided, by two deep grooves, into a median caruncle-like portion and two lateral areas (pl. 12, fig. 21). There are two tentacles (not shown in the figure) situated in deep depressions at the posterior end of the head. The median caruncle-like area is continued backward between the bases of the tentacles, ending in a slightly elevated free fold. Anterior to each tentacle the outer wall of the groove lies against the "caruncle," but just in front of each it bends abruptly outward and expands into an elevated wing-like outer wall to the tentacular pit. Each tentacle has an erect bulbous base and a gently tapering terminal

portion, which is deeply grooved on its dorsal surface and extends to the eighteenth setigerous somite. The anterior end of the "caruncle" is provided with a median papilla. The pharynx was partly protruded and showed a much pigmented inner surface. Eyes were not observed.

The peristomium is fused ventrally with the first setigerous somite so that the latter seems to be situated on top of the former. The ventral surface of the peristomium has numerous longitudinal grooves which converge toward the margin of the mouth. The lateral and dorsal lips are very rugose, possibly due to the partial protrusion of the pharynx.

The first setigerous somite is fused ventrally with the peristomium, while dorsally its posterior margin is even with the posterior edge of the tentacle. The neuropodium is a low papilla, having a postsetal lobe extending to the end of the setae. The notopodium, a rounded papilla, is much shorter than the neuropodium, and has small postsetal lobes and few setae.

The second setigerous somite is not entirely distinct from the peristomium on its ventral surface, but is more distinct laterally. The neuropodium is larger than that of the first somite but otherwise resembles it. The notopodium has a rounded presetal lobe and a flat, curved gill, which extends dorsally about as far as the middle of the tentacle. The anterior edge of the gill is smooth, while its posterior edge is convex and frilled.

The later parapodia increase in prominence and the postsetal lobes of both neuropodium and notopodium become thick vertical plates separated from one another only by a very narrow space (pl. 12, fig. 22). The body gradually alters its shape until, at the twenty-fifth somite, it assumes a rectangular form, its lateral surfaces being composed of the vertically arranged parapodia. The width of this rectangle is about twice its height. The gills in each parapodium are continuations of the postsetal notopodial plate. They become more nearly cylindrical toward the middle of the body, and lie close to the dorsal surface with their long axes at right angles to that of the body, leaving an uncovered area about equal to half of the diameter of the body.

The posterior end of only one specimen was found, and it lacked the pygidium. On this fragment the gills disappear quite abruptly at a considerable distance from the end, and the neuropodial and notopodial lobes are very small. The setae are arranged in a single vertical row in each lobe of the parapodium, the most dorsally placed noto-

podial tuft being the longest of any. Each seta curves gently to an acute apex. In formalin the body is a uniform light brown.

Type collected from Shumagin, Alaska; others from the Popof Islands of the Shumagin group.

Type in the Museum of the University of California; co-type in the American Museum of Natural History.

***Polydora californica* sp. nov.**

Pl. 12, figs. 23-29

This species is represented by an incomplete specimen having a body-width of rather less than one millimeter.

The head has a median "caruncle" which protrudes anteriorly beyond the margin of the head, and extends to between the bases of the tentacles. On either side of this "caruncle" there is a flattened wing-like area, and the apices of these two areas, together with the end of the median lobe, form the anterior margin of the head (pl. 12, fig. 23). On either side of the median lobe is a dark brown band of pigment. The tentacles are three millimeters long, or six times longer than the head, and their width, at their bases, is about one quarter that of the head. There are two pairs of small black eyes concealed by the bases of the tentacles.

The anterior end of the body is flattened dorsally, gills appearing on the second setigerous somite. At first these gills are lateral and those on opposite sides of the same somite are separated by a considerable space. In later somites they gradually approach the dorsal surface, becoming strictly dorsal in the fifteenth somite. The gills are at first very short, but increase in length up to the seventh pair, which meet on the mid-dorsal line. Toward the posterior end the gills are smaller and are entirely missing on at least the last eighteen somites.

The fifteenth and later somites are nearly circular in cross section, except at the very posterior end, which is again flattened. For the first fifteen somites the only color is in the gills, which are dark brown. From the fifteenth to the fiftieth somite the dorsal surface is light reddish-brown, broken by a median colorless band and by a similar colorless line marking the somite boundary. The remainder of the animal is colorless. The body noticeably narrows toward the posterior end but the pygidium was not preserved.

The first parapodium is inconspicuous and its notopodial setae lie just ventral to the bases of the tentacles. The neuropodium and notopodium are each provided with a postsetal lobe, that of the notopodium

being more conical and having a narrower base than that of the neuropodium. In the notopodium there is a dorsal tuft of three or four long slender setae, each of which gently tapers to an acute point and has a narrow wing towards its apex. There is also a ventral tuft of shorter setae, similar in form to the dorsal ones, but somewhat stouter. In the neuropodium there is a double row of stout, curved, and sharp-pointed setae, each having a narrow wing along its curved edge (pl. 12, fig. 24). All setae show a tendency to fray along the edges, possibly as a result of the pressure of the cover glass.

The second parapodium is essentially similar, in general outline and in character of setae, to the first, but is much more prominent. On its dorsal surface there is a short, thick, finger-shaped gill containing very prominent blood vessels. The third parapodium is similar to the second in outline, but its gill is somewhat larger (pl. 12, fig. 25). The relative lengths of the setae are shown in this figure, but not their form. The setae are similar to those of the anterior somites, but are covered with fine fuzzy processes, due either to a deposit from the outside, or to their breaking up.

The spines of the sixth setigerous somite are of two kinds; one (pl. 12, fig. 26) gently curved to a blunt point; the other broadened at its apex and cut across so that one edge is prolonged into a rounded flat region, from the base of which numerous hair-like processes arise (pl. 12, fig. 27). The base of each spine is dark brown and its apex is yellow. Behind this somite the ventral setae are replaced by hooks, each with a well developed hood (pl. 12, figs. 28, 29), while the dorsal setae are like those of the anterior somites.

The specimen was taken from a tangled mass of tubes apparently constructed by the *Polydora*. No locality was recorded.

Type in the Museum of the University of California.

Family CHAETOPTERIDAE

Chaetopterus variopedatus Renier

Tricoelia variopedatus Renier (1804).

Chaetopterus pergamentaceus Aud. et Milne Edwards (1834), p. 281, pl. 8, figs. 1-4.

Chaetopterus variopedatus Claparède (1869), p. 78.

Chaetopterus variopedatus Joyeux-Laffuie (1890), p. 347.

Chaetopterus variopedatus Enders (1909), p. 481.

The California specimens belong to the species commonly called *C. pergamentaceus*, but as Joyeux-Laffuie (1890) has shown, the

European *C. pergamentaceus* is synonymous with *C. variopedatus*. Enders (1909) concluded also that the species found on the eastern coast of the United States is *C. variopedatus*. I have compared the California specimens with a specimen from Naples, labeled *C. variopedatus*, and find no essential differences between them.

Frequent in collections from San Diego and San Pedro.

Family CIRRATULIDAE

***Cirratulus cingulatus* Johnson**

Cirratulus cingulatus Johnson (1901), p. 422, pl. 14, figs. 145-148.

Collected at Puget Sound; Pillar Point, California; Point Loma, San Diego.

***Cirratulus spirabranchnus* Moore**

Cirratulus spirabranchnus Moore (1904), p. 492, pl. 38, figs. 26-27.

Collected from Bolinas Bay; Pacific Grove; Santa Barbara; San Pedro; and also in haul LIV, on the sand bar at the entrance to San Diego Bay in 2 to 4 fathoms.

***Cirratulus robustus* Johnson**

Cirratulus robustus Johnson (1901), p. 423, pl. 14, figs. 149-150.

Collected from Kodiak Islands, Alaska; Bolinas Bay; Pacific Grove; and San Pedro.

***Cirratulus luxuriosus* Moore**

Cirratulus luxuriosus Moore (1904), p. 493, pl. 38, figs. 28-31.

The distinction between this species and *C. spirabranchnus* did not always seem to me to be clear. I have separated the two chiefly on the position of the gills, these being on the fourth setigerous somite in *C. luxuriosus* and on the seventh in *C. spirabranchnus*.

Collected from Pillar Point, California; Pacific Grove; White's Point and Terminal Island, near San Pedro; and also in haul XLI-4, in San Diego Bay in 2 to 3 fathoms on sand and broken shells.

***Cirratulus* sp. (?)**

Collected in haul LXX-5, off La Jolla in 54 to 118 fathoms on mud and soft black shale.

Tharyx multifilis Moore

Tharyx multifilis Moore (1909a), p. 267, pl. 9, fig. 43.

Collected from San Pedro and also in haul 1155, off La Jolla in 70 fathoms on green mud.

Chaetozona spinosa Moore

Chaetozona spinosa Moore (1903), p. 468, pl. 26, figs. 73-74.

Collected in haul XLII, in San Diego Bay in 3 to 7 fathoms on soft black mud; and in haul XLIII-1, in San Diego Bay in 3 to 7 fathoms on soft black mud.

Family MAGELONIDAE

Magelona longicornis Johnson

Magelona longicornis Johnson (1901), p. 414, pl. 11, figs. 115-118

Collected from Kumnes Point, and San Pedro.

Family AMMOCHARIDAE

Ammochares occidentalis Johnson

Ammochares occidentalis Johnson (1901), p. 420, pl. 14, figs. 140-142.

Collected from Sitka Harbor, Alaska; and Timm's Flats and Sand Flats near San Pedro.

Family TEREHELLIDAE

Amphitrite palmata Moore

Amphitrite palmata Moore (1905c), p. 858, pl. 44, figs. 19-22.

Collected from Yakutat, Alaska.

Amphitrite spiralis Johnson

Amphitrite spiralis Johnson (1901), p. 426, pl. 16, figs. 169-171c.

Collected from Port Orchard, Channel Rocks, and Pleasant Beach in Puget Sound; Trinidad; Patrick's Point, Humboldt County; Santa Barbara; Point Loma and vicinity in San Diego Bay; and Coronado. Also in shore collection at Station VIII at San Pedro.

Amphitrite robusta Johnson

Amphitrite robusta Johnson (1901), p. 425, pl. 16, figs. 164-168.

Collected from Port Orchard and Pleasant Beach in Puget Sound; Patrick's Point, Humboldt County; Lime Point, San Francisco Bay;

San Pedro; and San Diego Bay. Collected also in haul LXVII, off San Diego in 19 to 31 fathoms on grayish-yellow sand; and in haul LXX-5, off La Jolla in 54 to 118 fathoms on green mud and soft black shale.

***Terebella californica* Moore**

Terebella (*Schmardanella*) *californica* Moore (1904), p. 496, pl. 38, figs. 36-37.

Collected from Pillar Point, California; San Pedro; and False Bay, and Point Loma near San Diego.

***Terebella* sp. (?)**

Tubes only, collected in haul 1555, off San Clemente Island in 50 fathoms on coarse sand.

***Lanice heterobranchia* Johnson**

Lanice heterobranchia Johnson (1901), p. 427, pl. 17, figs. 172-174.

Collected from Puget Sound; Patrick's Point, Humboldt County; Trinidad; Cape Mendocino; Tomales Bay; Pillar Point, California; Pacific Grove; San Pedro; and San Diego Bay. Collected also in the following hauls: XLVI-2, off Coronado in 5 to 6 fathoms on sand; LIX, off the Coronado Islands in 15 fathoms on fine gray sand; LXXXII-1, off Point Firmin in 27 to 30 fathoms on fine gray sand.

***Thelepus crispus* Johnson**

Thelepus crispus Johnson (1901), p. 428, pl. 17, figs. 175-178b.

All of these agreed with Johnson's description in the character of gills and setae, and in the general form of the body. I did not find uncini in two rows in any somite, and the body is apt to narrow posteriorly more than is stated in Johnson's description. The number of posterior somites free from setae was greater than in Johnson's description.

Collected from Yakutat and Neah Bay, Alaska; Puget Sound; Cape Mendocino; Bolinas, Duxbury Reef; Point Cavallo, San Francisco Bay; Pillar Point, California; Pacific Grove; Deadman's Island, White's Point, and Timm's Point near San Pedro; Avalon, Santa Catalina Island; False Bay, near San Diego; Point Loma, Zuninga Point, and Ballast Point in San Diego Bay; and San Clemente Island. Collected also in haul L-1, off San Diego in 21 to 28 fathoms on rocks; in haul LXXXIII, off San Pedro in 110 to 240 fathoms on sand and broken shells; and in haul 1238, on sand flats in San Diego Bay.

Thelepus hamatus Moore

Thelepus hamatus Moore (1905c), p. 856, pl. 44, figs. 16-18.

Collected in haul XXVI-1, off Santa Catalina Island in 46 to 49 fathoms on sand.

Pista alata Moore

Pista alata Moore (1909a), p. 273, pl. 9, figs. 48-51.

Collected from San Pedro; San Diego; and San Clemente Island. Collected also in the following hauls: XIV-1, off San Pedro in 40 to 155 fathoms on soft sticky mud; XIX-1, off San Pedro in 30 to 100 fathoms on soft mud, sand, and pebbles; L-1, off San Diego on a rocky bottom in 21 to 28 fathoms; 1102, off La Jolla in 15 to 35 fathoms on sand, mud, and broken shells; 1157, off La Jolla in 160 fathoms on green mud.

Pista elongata Moore

Pista elongata Moore (1909a), p. 270, pl. 9, figs. 45-47.

Collected from San Diego and San Clemente Island.

Pista typha Grube

Pista typha Grube (1878), p. 232, pl. 12, fig. 4.

Collected in haul 1157, off La Jolla in 160 fathoms on green mud.

Pista sp.(?)

Collected in haul LXX-5, off La Jolla in 54 to 118 fathoms on mud and soft black shale; and in haul LXX-6, off La Jolla in 54 to 125 fathoms on mud, sand, and soft black shale.

Polycirrus californicus Moore

Polycirrus californicus Moore (1909a), p. 276, pl. 9, figs. 52-53.

Collected from Portuguese Bend; San Pedro; and Coronado.

Streblosoma crassibranchia sp. nov.

Pl. 12, figs. 30, 31

The definition of this species is provisional, for it depends upon a single imperfect specimen. Its total length was twelve millimeters and its greatest width not more than one millimeter.

The prostomium is prominent and its sides are folded almost at right angles to its dorsal portion so that, together with the lower lip, they enclose a rectangular area. The lower lip is fleshy and rather prominent. The tentacular ridge is moderately developed, with a dense row of minute dark spots extending to the ends of the lower lip. The tentacles are more than one-third longer than the body and the width of each, at its base, is about one-eighth that of the body; they narrow very little toward their ends. The specimen had six tentacles in a row on the right and five on the left. The two most ventral ones of the left row were very small, and were possibly regenerating. There are three pairs of cirriform gills. The anterior pair have five cirri on either side, extending to the base of the tentacles. The middle pair have four cirri on either side, and are slightly more than half as long as the anterior pair. The posterior pair are nearly as long as the middle pair and have three cirri on the left and one on the right. It is not probable that these numbers are constant.

Setae begin on an elevated ridge on the second somite and extend for eighteen somites. The body, behind this point, was much smaller than anteriorly and no setae were seen on it. It was possibly regenerating. The setae (pl. 12, fig. 30) are short with lance-shaped ends, and are arranged in a dense bundle. The uncinus is provided with a large terminal hook, and the crest is composed of two larger lateral and three smaller median teeth (pl. 12, fig. 31).

Locality (?). Type in the Museum of the University of California.

Family AMPHARETIDAE

Amage tumida Ehlers

Amage tumida Ehlers (1887), p. 220, pl. 48, figs. 10-19.

These differ from Ehler's description in the number of somites, but it seems best to list the three specimens in the collection with Ehler's species.

Collected in haul 1112, off La Jolla in 45 fathoms on green mud and fine sand; and in haul 1123, off La Jolla on a muddy bottom in 160 fathoms.

Amphictels alaskensis Moore

Amphictels alaskensis Moore (1905c), p. 846, pl. 44, figs. 1-4.

Collected in haul LXX-5, off La Jolla in 54 to 118 fathoms on mud and soft black shale.

***Amphicteis japonica* McIntosh**

Amphicteis japonica McIntosh (1885), p. 431, pl. 27a, figs. 3-5.

Collected in haul LXX-6, off La Jolla in 54 to 125 fathoms on mud, sand, and soft black shale; and in haul LXXIII-1, off San Diego in 106 to 132 fathoms on fine gray sand.

***Amphicteis glabra* Moore**

Amphicteis glabra Moore (1905c), p. 849 pl. 44 figs. 5-8.

Collected in the following hauls: XIV-3, off San Pedro in 40 to 150 fathoms on gray mud; XLII-1, in San Diego Bay in 3 to 7 fathoms on soft black mud; LXXIII-1, off San Diego in 106 to 132 fathoms on fine gray mud; LXXIV, in San Diego Bay in 1 to 2 fathoms on mud and broken shells; 1124 and 1157, off La Jolla on a muddy bottom in 160 fathoms.

***Amphicteis scaphobranchiata* Moore**

Amphicteis scaphobranchiata Moore (1906), p. 255, pl. 12, figs. 54-61.

In minor details these differ from Moore's description. The paleoli often taper, at the end, in much more abrupt fashion than he figures, and the peristomium shows transverse wrinkles on its dorsal surface. The peculiarly shaped median branchia, which Moore thought might not be normal, has this form wherever it appears, and is apparently perfectly normal.

Collected in the following hauls: XII-2, off San Pedro in 35 to 175 fathoms on black asphalt rocks, pebbles, coarse sand, and broken shells; XVIII, off San Pedro in 17 to 33 fathoms on sand and mud; XLII, in San Diego Bay in 3 to 7 fathoms on soft black mud; LXX-6, off La Jolla in 54 to 125 fathoms on mud, sand, and soft black shale.

***Ampharete arctica* Malmgren**

Ampharete arctica Malmgren (1864), p. 364, pl. 26, figs. 77-77d.

Collected in haul VI-1, in the outer San Pedro Harbor in 9 fathoms on gray sand.

***Melinna denticulata* Moore**

Melinna cristata Moore (1905c), p. 851, pl. 44, figs. 9-10 (name preoccupied).

Melinna denticulata Moore (1908b), p. 349.

Collected in haul LXXX-1, off San Diego in 135 fathoms on fine greenish-gray mud and sand; and in haul 1157, off La Jolla on a muddy bottom in 160 fathoms.

Sabellides anops Johnson

Sabellides anops Johnson (1901), p. 424, pl. 15, figs. 157-161; pl. 16, figs. 162-163.

Collected from San Pedro; in haul 1102, off La Jolla in 15 to 35 fathoms on sand, mud, and broken shells; and in haul 1124, off La Jolla on a muddy bottom in 160 fathoms.

Sabellides auricula Malmgren

Amage auricula Malmgren (1864), p. 371, pl. 25, figs. 72-72d.

Collected in haul LXXIII-3, off San Diego in 57 to 106 fathoms on dark-green mud and fine sand.

Family AMPHICTENIDAE

Pectinaria brevicoma Johnson

Pectinaria brevicoma Johnson (1901), p. 423, pl. 15, figs. 151-156.

Collected from Berg Bay, Glacier Bay, Wrangell, and Kodiak Islands in Alaska; Santa Barbara; and San Pedro. Collected also in the following hauls: X, off San Pedro on a muddy bottom in 19 to 38 fathoms; XIV-1, off San Pedro in 40 to 155 fathoms on soft, sticky mud; XIV-2, off San Pedro in 25 to 240 fathoms on greenish-brown mud and gray sand; XIV-3, off San Pedro in 40 to 150 fathoms on gray mud; XVIII, off San Pedro in 17 to 33 fathoms on sandy mud; XX, off San Pedro in 50 to 100 fathoms, bottom not recorded; XLII, in San Diego Bay in 3 to 7 fathoms on soft black mud; XLIII-1, in San Diego Bay in 3 to 7 fathoms on soft black mud; XLIII-2, in San Diego Bay in 5 to 8 fathoms on soft black mud; LXII, off San Diego in 16 to 18 fathoms on gray sand; LXX-1, off La Jolla in 56 to 137 fathoms on rocks; LXX-5, off La Jolla in 54 to 118 fathoms on mud and soft black shale; LXX-6, off La Jolla in 54 to 125 fathoms on mud, sand, and soft black shale; LXXII-3, off San Diego in 45 to 50 fathoms on foul, dark-green mud; LXXIII-1, off San Diego in 106 to 132 fathoms on fine gray sand; LXXIII-2 and 3, off San Diego in 57 to 106 fathoms on green mud and sand; LXXX-2, off San Diego in 125 fathoms on fine mud and sand; LXXXII-2, off Point Firmin in 30 to 31 fathoms; 1112, off La Jolla in 45 fathoms on green mud and fine sand; 1122, off La Jolla in 100 fathoms on green mud and fine sand; 1124 and 1157, off La Jolla on a muddy bottom in 160 fathoms.

Cistenides hyperborea Malmgren

Cistenides hyperborea Malmgren (1864), p. 360, pl. 18, figs. 40-40e.

Collected from Kodiak Islands in Alaska.

Family CAPITELLIDAE

Dasybranchus glabrus Moore

Dasybranchus glabrus Moore (1909a), p. 280, pl. 9, fig. 58.

Moore's description was based on a single specimen forty-five millimeters long. The specimens in the collections which seem to belong to this species were much longer, some sexually mature forms measuring three hundred millimeters. The inflated hoods surrounding the ends of the abdominal crochets are not smooth as figured by Moore, but, instead, each has a transverse row of short sharp teeth on its end.

Collected from Deadman's Island; San Pedro; and San Clemente Island.

Dasybranchus giganteus Moore

Dasybranchus giganteus Moore (1909a), p. 278, pl. 9, fig. 56.

Collected from Coronado and San Clemente Island.

Notomastus tenuis Moore

Notomastus tenuis Moore (1909a), p. 277, pl. 9, fig. 55.

Locality unknown.

Family CHLORHAEMIDAE

Trophonia papillata Johnson

Trophonia papillata Johnson (1901), p. 416, pl. 12, figs. 122-123.

Collected from Trinidad; Shelter Cove; Tomales Bay; La Jolla; and San Diego. Collected also in haul XLII, in San Diego Bay in 3 to 7 fathoms on soft black mud; and in haul LXX-7, off La Jolla on a rocky bottom in 55 to 125 fathoms.

Trophonia capulata Moore

Trophonia capulata Moore (1909a), p. 284, pl. 9, figs. 60-61.

Collected from Portuguese Bend; and in haul X, off San Pedro on a muddy bottom in 19 to 38 fathoms.

***Trophonia minuta* sp. nov.**

Pl. 12, fig. 32

Total length not over fifteen millimeters. Its much flattened anterior end was smoothly beveled dorsally, and covered with fine sand-grains. The remainder of the body is circular in outline on cross-section and of nearly uniform diameter back to about the twenty-fifth somite, where it abruptly narrows to not more than a quarter of its former width. There is a row of inconspicuous papillae along the anterior dorsal edge of each somite, and the first six or seven somites have a similar row of minute papillae along their anterior ventral edges. Otherwise the whole surface of the somites is smooth. The posterior end of the animal was lacking in all specimens.

Anterior tufts of setae are prominent and half as long as the entire body. The dorsal setae of the remainder of the body are very short, fine, delicate, and capillary, but otherwise essentially like the anterior setae in form. There are three ventral hooks in a vertical row on each somite, the most dorsal one being the longest, while the two others are successively shorter and stouter (pl. 12, fig. 32). The head was retracted in all specimens.

Moore (1909a, p. 284) lists *Trophonia papillata*, Johnson, and notes that one specimen was small and poorly preserved, possibly being a new species. *T. minuta* is probably the same species as this new one mentioned by Moore, and differs from other California *Trophonia* thus far described in the very feeble development of the papillae. That they are adults and not, as I at first supposed, immature forms is shown by the fact that one was full of eggs.

Collected in haul 1147, off La Jolla in 10 fathoms.

Type in the Museum of the University of California; co-type in the American Museum of Natural History.

***Trophonia inflata* sp. nov.**

Pl. 12, fig. 33

The type is eighteen millimeters long and five millimeters wide at about one-fourth of its length behind the head. The diameter of the head is about four millimeters. The posterior end of the body is very narrow, barely 0.5 mm. wide at its end. This inflated condition is unusual and may be due to the method of preservation. The anterior setae are delicate and about twelve millimeters long. The

tentacles are very slender and one-third as long as the anterior setae. They are apparently unequal in size and their exact number was not easy to determine in preserved material. The palps are much thicker than the tentacles and one-half as long as the longest one. Each is provided with lobulated edges and a ventral groove.

The anterior end is noticeably truncated dorsally, the truncated portion being covered with a dense layer of sand grains. A much thinner outer coating covers the remainder of the body, the papillae being clearly seen through it. For about the first ten somites these papillae form a fringe along the anterior border of each somite. Farther back the papillae become less prominent and are distributed over most of the surface of the somite. Larger papillae are arranged so that those of successive somites form a row about midway between the neuropodium and the mid-ventral line on either side. Another series of papillae form an incomplete row on either side, ventral to the others. On the ventral margin of the head there are about six prominent papillae just ventral to the palps. The dorsal papillae are essentially similar to the lateral and ventral ones, except that none is especially prominent. Clumps of papillae accompany the setae tufts, the largest forming a longitudinal row ventral to the neuropodium.

The anterior neuropodial setae are slender and elongated, their joints being six to eight times longer than broad. Farther back they become exceedingly delicate, and are especially liable to be lost when the sandy covering of the body is scraped away. The notopodial setae are also very delicate at the anterior end of the body, but are replaced by hooks at about the sixth somite. These are at first arranged in transverse rows of three or four, but the number becomes smaller toward the posterior end. The hooks (pl. 12, fig. 33) are pale yellow with smooth bases. Each gently curves toward its bluntly rounded apex, and is without accessory processes.

The type was collected from Santa Catalina Island. Others were collected from Portuguese Bend; San Diego; and in haul L-1, off San Diego on a rocky bottom in 21 to 28 fathoms.

Type in the Museum of the University of California; co-type in the American Museum of Natural History.

***Flabelligera infundibularis* Johnson**

Flabelligera infundibularis Johnson (1901), p. 417, pl. 12, figs. 124-127.

Collected from Yakutat and Kodiak Islands, Alaska; and Scow Bay and other points in Puget Sound.

***Brada pilosa* Moore**

Brada pilosa Moore (1906), p. 231, pl. 10, figs. 14-17.

Collected in the following hauls: XLII and XLIII-1, in San Diego Bay in 3 to 7 fathoms on soft black mud; XLIII-3, in San Diego Bay in 5 to 8 fathoms on soft black mud.

***Brada granulata* Malmgren**

Brada granulata Malmgren (1867), p. 194, pl. 13, figs. 71-71d.

Collected at Orca in Prince William Sound, Alaska.

Family STERNASPIDAE

***Sternaspis fossor* Stimpson**

Sternaspis fossor Stimpson (1853), p. 29, fig. 19.

Abundant in the collections, and apparently identical with the Atlantic species. Collected from Sitka, Alaska, and in the following hauls: X, off San Pedro on a muddy bottom in 19 to 38 fathoms; XII-2, off San Pedro in 35 to 175 fathoms on black asphalt rocks, pebbles, coarse sand, and broken shells; XIII, off San Pedro on a sandy bottom in 35 to 36 fathoms; XIV-2, off San Pedro in 25 to 240 fathoms on greenish-brown mud and gray sand; XIX-3, off San Pedro in 30 to 77 fathoms on soft mud, coarse sand, and pebbles; XX, off Santa Catalina Island in 50 to 100 fathoms; XXI-1, off Santa Catalina Island in 43 to 58 fathoms on green mud, sand, and pebbles; XXX-1, off Santa Catalina Island in 62 fathoms on rock; XXXV, off Ballast Point, Santa Catalina Island in 6 to 30 fathoms on green mud; LXX-5, off La Jolla in 54 to 118 fathoms on mud and soft black shale; LXXI, off La Jolla on a muddy bottom in 15 to 56 fathoms; LXXIII-2 and 3, off San Diego in 57 to 106 fathoms on green mud and sand; LXXX-2, off San Diego in 125 fathoms on mud and fine sand; 1102, off La Jolla in 15 to 35 fathoms on sand, mud, and broken shells; 1112, off La Jolla in 45 fathoms on green mud and fine sand; 1145, off La Jolla on a muddy bottom in 30 fathoms.

Family OPHELLIDAE

***Travisia pupa* Moore**

Travisia pupa Moore (1906), p. 228, pl. 11, fig. 23.

Collected in the following hauls: XII-2, off San Pedro in 35 to 175 fathoms on black asphalt rocks, pebbles, coarse sand, and broken

shells; XIV-2, off San Pedro in 25 to 240 fathoms on greenish-brown mud and gray sand; XIX-3, off San Pedro in 30 to 77 fathoms on soft mud, coarse sand, and pebbles; LXX-3, off La Jolla in 55 to 108 fathoms on rocks and fine mud; LXXII-2, off San Diego in 47 to 51 fathoms on soft gray mud; LXXII-4, off San Diego in 36 to 47 fathoms on mud; LXXIII-3, off San Diego in 57 to 106 fathoms on dark-green mud and sand; 1157, off La Jolla on a muddy bottom in 160 fathoms; 1475 and 1497, off La Jolla on a sandy bottom in 50 to 100 fathoms.

***Ammotrypane brevis* Moore**

Ammotrypane brevis Moore (1906), p. 354, fig. 1.

Collected from San Pedro.

***Ammotrypane gracile* McIntosh**

Ammotrypane gracile McIntosh (1885), p. 357, pl. 43, figs. 9, 12.

Collected from Pacific Grove; Deadman's Island, San Pedro; San Diego; and Coronado. Collected also in the following hauls: XXXIV, off Santa Catalina Island in 90 to 125 fathoms on green mud and sand; LXXIII-3, off San Diego in 57 to 106 fathoms on dark-green mud and sand; 1112, off La Jolla in 45 fathoms on green mud and fine sand.

***Polyophthalmus australis* Grube**

Polyophthalmus australis Grube (1878), p. 196, pl. 10, fig. 4.

Collected from White's Point and vicinity near San Pedro; and in haul LXXVIII, from the piles of the Santa Fé wharf in San Diego Bay.

***Ophelina magna* sp. nov.**

Pl. 12, figs. 34-36

The body is ninety millimeters long and eight millimeters wide at its widest point, the sixth setigerous somite. There are forty-eight somites and thirty-one pairs of gills, the first pair being on the eleventh somite.

The prostomium is smooth and bluntly conical (pl. 12, fig. 34). On either side of its base is a prominent sensory pit. The peristomium is marked, dorsally, by a longitudinal groove on either side, which is continued posteriorly into a groove just dorsal to the setae

tufts. Its dorsal surface is also marked with transverse annulations, the posterior border of each slightly overlapping the one behind it so as to resemble clapboards. These annulations are found in succeeding somites, but their overlapping is less marked posteriorly.

The mouth has prominent anterior and posterior lips. Two grooves, appearing at the base of the prostomium, diverge to pass along the lateral edges of the mouth and, continuing posteriorly, form the lateral edges of the ventral "sole." Both dorsal and ventral lips are provided with many small scale-like epidermal thickenings arranged in rows resembling the pavement teeth of an elasmobranch.

The ventral surface of each of the first seven setigerous somites is flat, and divided on either side by a longitudinal furrow. Behind the seventh somite the whole surface of each is much depressed, forming, in preserved material, a deep longitudinal groove which extends to the posterior end of the body. All somites are annulated. Anteriorly, each has three annulations, of which the first and third are biannulate on the dorsal surface. The ventral surface retains the triannulate condition throughout the entire body except for the last four or five somites, where it disappears. Dorsally, the surface first becomes quadriannulate, then biannulate, and the annulations finally disappear entirely in the last nine somites.

The anus is posterior and is surrounded by a ring of about thirty cirri, of which the two ventral ones are much longer than the others. The cirri are thick and almost spherical in form.

On the ninth and tenth setigerous somites there are numerous small glands, the openings of which extend nearly to the mid-dorsal line. They are especially numerous on the tenth somite, where the skin containing them shows a swollen area.

The parapodia have two thick presetal lobes throughout the body. The setae of the first setigerous somite are arranged in a dorsal and ventral bundle, each containing about fifteen. Each dorsal seta is long and curves gently to a moderately acute apex. Each has a narrow wing on its convex surface which does not continue to its apex (pl. 12, fig. 35). The basal portion of each has minute longitudinal striations. Most of the ventral setae were broken, but those which remained were similar in form to the dorsal ones.

Farther back, the setae become more prominent (pl. 12, fig. 36, a parapodium of the 14th somite). Ventrally there is a tuft of setae essentially like those of the first setigerous somite. At first the dorsal tuft has a few setae like those of the ventral tuft, but, dorsal to these.

are some very long thread-like setae which extend beyond the apex of the gill. These thread-like setae are noticeably longitudinally striated, but have no lateral wing.

Each gill is finger-shaped and much wrinkled (possibly a result of preservation). They are of uniform length throughout except for the last pair, which are noticeably smaller. Dorsal to the gills are many small spots, apparently the openings of epidermal glands.

Collected in the following hauls: VI-1, in the outer San Pedro Harbor in 3 fathoms on gray sand; XXXII, off Santa Catalina Island in 12 to 40 fathoms on green mud and sand; XLI-1 to 3, in San Diego Bay in 2 to 3 fathoms on coarse sand and broken shells; 252, in San Diego Bay in 3 to 5 fathoms on sand and mud. The type was from an unknown locality.

Type in the Museum of the University of California; co-type in the American Museum of Natural History.

***Ophelina mucronata* sp. nov.**

Pl. 12, figs. 37, 38

The length of specimens of this species varies with the degree of expansion. A slender one, apparently much expanded, measured thirty-five millimeters in length, and barely one millimeter in width, while the type was twenty-five millimeters long and two millimeters wide.

The head is almost an equilateral triangle having rounded basal angles and an apex prolonged into a short sharp-pointed process. There is a pair of very faintly indicated sensory spots on its dorsal surface (pl. 12, fig. 37). The mouth is situated barely one-half the length of the head behind its apex. The pharynx, when protruded, consists of three broad foliaceous lobes. Behind the mouth the ventral surface of the head is very much swollen. The first setigerous somite is not sharply separated from the prostomium, and that portion anterior to the seta tuft is broader than the rest and continuous with the swollen sides of the head, so that the first setae apparently arise at the boundary between the swollen head and this somite. The setae of the first tuft are more prominent than of the immediately following ones.

The body consists of about thirty-four somites, though it is not easy to be accurate on this point because of the difficulty in discerning the somite boundaries towards the posterior end of the body. For the first twelve setigerous somites the body is nearly circular in cross-

section, its ventral surface is flattened, and its somite boundaries are indistinct and marked, chiefly, by the position of the setae tufts. On either side of the ninth somite there is a vertical torus-like glandular swelling. Gills begin on the twelfth somite and the body changes in appearance, due to the occurrence of a deep ventral and two shallow lateral grooves. Its dorsal surface is more convex and is provided with definitely arranged transverse markings which, in the non-pigmented forms, appear as five narrow white bands in each somite, the one nearest the gill being the largest. Behind the last pair of gills the lateral grooves become less prominent and the whole body enlarges. In preserved material, the terminal portion of the body appears as a narrow, three-ringed area invaginated into a swollen area just anterior to it. On either side, this carries a bundle of long, delicate, and pointed setae. The pygidium has a ventral cirrus. The base of the cirrus is half as wide as the pygidium and its sides are rounded and rapidly narrow, ending in a blunt-pointed finger-shaped process. On either side of this process the edge of the pygidium is prolonged into seven slender cirri.

There are eighteen pairs of gills. They are apparently capable of contraction, since they are relatively longer in the type than in other specimens (pl. 12, fig. 38, from co-type). They are bifid and much wrinkled.

The setae of the first tuft are more prominent than those of the immediately following tufts, which are, however, easily seen as far back as the first gill-bearing somite. Here they are very small, and are visible only under considerable magnification. They are situated in two tufts at the base of the gill. The ventral setae are shorter, and the dorsal ones are slightly longer, than the diameter of the gill (pl. 12, fig. 38). As shown in the figure they arise directly from the body-wall, without any noticeable parapodia. All the setae are simple, long, narrow and tapering.

Collected from La Jolla in sand.

Type in the Museum of the University of California; co-type in the American Museum of Natural History.

Family MALDANIDAE

Clymenella rubrocincta Johnson

Clymenella rubrocincta Johnson (1901), p. 418, pl. 13, figs. 128-133.

Collected from Puget Sound; Tomales Bay; Pacific Grove; San Pedro; and San Diego. Collected also in the following hauls: XLV,

along the rocky shore of San Diego Bay; LIX, off the Coronado Islands in 15 fathoms on fine gray sand; 1124, off La Jolla on a muddy bottom in 160 fathoms; 1155, off La Jolla on a muddy bottom in 70 fathoms.

Maldane sarsii Malmgren

Maldane sarsii Malmgren (1865), p. 188.

Collected in the following hauls: LXX-5, off La Jolla in 54 to 118 fathoms on mud and soft black shale; 1122, off La Jolla in 100 fathoms on green mud and fine sand; 1157, off La Jolla on a muddy bottom in 160 fathoms; 1475, off La Jolla on a sandy bottom in 50 to 100 fathoms.

Maldane similis Moore

Maldane similis Moore (1906), p. 233, pl. 11, figs. 26-30.

Collected in haul 1475, off La Jolla on a sandy bottom in 50 to 100 fathoms; and in haul 1486, off Oceanside in 403 fathoms on green mud. The specimen obtained in this haul is doubtfully referred here. If it belongs to this species it was immature.

Maldane disparidentata Moore

Maldane disparidentata Moore (1904), p. 494, pl. 38, figs. 28-31.

Collected from Pacific Grove; Timm's Flats near San Pedro; and Coronado. Collected also in the following hauls: XIV-3, off San Pedro in 40 to 150 fathoms on gray mud; XIX-2, off San Pedro in 30 to 77 fathoms on soft sandy mud and pebbles; LXXIV, in San Diego Bay in 1 to 2 fathoms on mud and broken shells; LXXV-1, in San Diego Bay on a muddy bottom in 2 to 3 fathoms.

Clymene mirabilonga Moore

Clymene mirabilonga Moore (1903), p. 480, pl. 27, figs. 89-93.

Collected from San Pedro and in the following hauls: X, off San Pedro in 19 to 38 fathoms on green mud; LXX-5, off La Jolla in 54 to 118 fathoms on mud and soft black shale.

Isocirrus sp. (?)

Collected in haul LXX-7, off La Jolla in 55 to 125 fathoms on soft black shale.

Family SCALIBREGMIDAE

Sclerocheilus pacificus Moore

Sclerocheilus pacificus Moore (1909a), p. 282, pl. 9, fig. 59.

I have identified a number of specimens as belonging to this species, though agreeing with Moore that they differ widely from the type of the genus. I was unable to find the furcate setae which are described and figured by Moore as characteristic of the species.

Collected from Avalon, Santa Catalina Island.

Family ARENICOLIDAE

Arenicola claparedii Levinson

Arenicola claparedii Levinson (1883), p. 136.

Collected from Dutch Harbor, Unalaska; and Alki Point, Puget Sound.

Family SABELLIDAE

Sabella elegans Bush

Sabella elegans Bush (1904), p. 194, pl. 26, fig. 2; pl. 27, fig. 6c; pl. 33, figs. 20-21; pl. 34, figs. 1, 4, 5, 10; pl. 37, figs. 12-33.

Locality unknown.

Potamilla acuminata Moore

Potamilla acuminata Moore (1904), p. 159, pl. 12, fig. 41.

Collected in haul L-1, off San Diego on a rocky bottom in 21 to 28 fathoms; one specimen from an unknown locality.

Myxicola pacifica Johnson

Myxicola pacifica Johnson (1901), p. 431, pl. 19, figs. 193-198.

Collected from Santa Barbara, San Pedro, and also in the following hauls: V-1, off San Pedro in 11 to 16 fathoms; XV, off San Pedro in 4 to 7 fathoms on coarse sand; XVI-2, off San Pedro in 9 fathoms on small rocks and pebbles; LXXXII-1, off Point Firmin in 27 to 30 fathoms on fine gray sand.

Parasabella media Bush

Parasabella media Bush (1904), p. 200, pl. 27, figs. 3-5; pl. 33, figs. 34-36; pl. 34, fig. 3; pl. 36, figs. 13-14; pl. 37, fig. 30.

Locality unknown.

Metachone mollis Bush

Metachone mollis Bush (1904), p. 216, pl. 35, figs. 19, 20, 28.

Collected in haul XLIII-1, in San Diego Bay in 3 to 7 fathoms on soft black mud.

Laonome punctata Treadwell

Laonome punctata Treadwell (1906), p. 1178, figs. 76, 77.

Collected from Honolulu.

Laonome oculifera sp. nov.

Pl. 12, figs. 39-43

The body, without the gills, is twenty millimeters long. It is six millimeters wide at its widest point, the thorax. The thoracic region is slightly flattened, while the abdomen is more nearly rounded, gradually tapering to its end. The thorax consists of eight somites and the abdomen of about sixty. The collar is two-lobed and rather prominent. Its edge is entire and its parts widely separated dorsally, while its ventral free ends are prolonged into slightly rolled edges, those of the two sides being in contact. The color, in alcohol, is a uniform light brown, the gills being somewhat lighter than the rest of the body. No colored spots occur except the eyes on the radioles.

There are about twenty-four radioles on a side arising from a prominent base which is slightly coiled ventrally. There are two rows of barbs on the inner face of each radiole. They are largest near its base, becoming very small toward its apex. The basal ones are black and the others are colored like the radiole. Each radiole has from one to five prominent light brown eyes on its dorsal surface.

The faecal groove is prominent in the abdomen. It bends to the right of the animal at the posterior end of the eighth somite, where it continues to the dorsal surface. Ventral scutes are prominent on all somites, the first thoracic one being much the largest. Its middle length is almost half its width, while that of the other thoracic scutes is only one-fifth their width. All of these, and six or seven anterior abdominal ones, tend toward a biannulate condition. The remaining scutes are about three times broader than long and each is equally divided by the faecal groove.

There are two sorts of setae on the collar fascicle. Dorsally, there is a bundle of long, gently tapering, sometimes slightly curved setae, each of which has a wing on either side (pl. 12, fig. 39). Ventrally

the setae are shorter and relatively broader than the dorsal ones, each with an asymmetrical wing at its end and numerous striations on its surface (pl. 12, fig. 40). While the most dorsal setae of the other thoracic somites are much like those of the collar setae, the ventral ones have orbiculate ends (pl. 12, fig. 41). The thoracic torus is provided with a row of large hooked uncinae, the apex of each being finely striated but hardly produced into definite teeth, while the basal portion of each is rounded and prolonged backward into a basal rod (pl. 12, fig. 42). Parallel to these uncinae is a row of pennoned setae (pl. 12, fig. 43). The abdominal setae are similar to those of the ventral part of the collar. The uncinae are like those of the thorax, but without pennoned setae.

Collected from San Pedro.

Type in the Museum of the University of California.

***Branchiomma disparoculatum* sp. nov.**

Pl. 12, figs. 44-46

The type is thirty-five millimeters long; its thorax is seven millimeters long; and its gills are also seven millimeters long. Its body is not over four millimeters wide in the widest portion of the thorax, and its abdomen is of uniform diameter except at its extreme posterior end, where it narrows abruptly. There are about twenty-one gills on each side, which are frequently broken and but slightly rolled at their bases. Radioles have barbs extending to their very ends except in those provided with eyes, when their tips are without them. In one pair of radioles, each carries a large subterminal eye, while a variable number of other radioles carry smaller ones which, in some cases, are hardly larger than a speck of pigment. The buccal membrane consists of two pairs of thin, leaf-like processes, of which the ventral one continues, as a thin lamella, to the ventral surface of the body between the collar lobes. The ends of the collar are slightly separated dorsally and the dorsal part of the collar, while thick, is inconspicuous owing to the rather sudden transition to its thin portion. This thin part forms a fold which partly overlaps the thick portion and is then continued without a break to the ventral surface where each side terminates in a triangular fold extending beyond the bases of the gills.

The thorax consists of eight somites and is provided with rather prominent ventral shields whose width is one-third that of the body.

There is a single tuft of curved, sharp-pointed collar setae, each of which has a terminal wing-like expansion (pl. 12, fig. 44). In profile, this expansion looks like a lateral wing; seen in full face, it shows on both sides of the central axis and is apparently a thin globular expansion which tapers to a point at its apex. The setae in other thoracic fascicles are of two kinds, one similar to those of the collar while the other kind are shorter and orbicular (pl. 12, fig. 45). Thoracic tori are provided with uncini and pennoned setae. The uncinus has a short base, one large tooth, and an apex with minute striations (pl. 12, fig. 46). Pennoned setae of the usual type are present but have rather larger terminal expansions.

Abdominal ventral shields are as prominent as the thoracic shields and, relatively, somewhat wider. The faecal groove crosses the shield of the first abdominal somite, and divides all subsequent ones equally. Abdominal setae are much longer than the thoracic ones. Abdominal uncini are much like thoracic ones, but their bases are apt to have a brown color. Terminal tooth very prominent, crest prominent, with numerous striations, but not showing separate teeth.

Collected from Honolulu Harbor, San Pedro, and San Diego. The type was labelled haul 9, off San Diego, but, as that haul was made with a no. 20 net towed in 70 fathoms, it is probable that the label was erroneously marked. Co-types also from San Diego. Specimens from Honolulu had tubes covered with minute fragments of shells and skeletons of Foraminifera, while some from San Pedro had tubes covered with fine sand.

Type in the Museum of the University of California; co-type in the American Museum of Natural History.

***Pseudopotamilla ocellata* Moore**

Pseudopotamilla ocellata Moore (1905b), p. 559, pl. 37, figs. 8-14.

Collected from Fort Ross Cove; Lime Point, San Francisco Bay; and in the following hauls; LXVIII, off San Diego in 19 to 30 fathoms on green mud and sand; LXXXII-1, off Point Firmin in 27 to 30 fathoms on fine gray sand.

***Pseudopotamilla brevibranchiata* Moore**

Pseudopotamilla brevibranchiata Moore (1905b), p. 555, pl. 37, figs. 1-7.

Collected from San Pedro.

Pseudopotamilla debilis Bush

Pseudopotamilla debilis Bush (1904), p. 204, pl. 36, figs. 23, 24, 26.

Collected in haul 1202, off La Jolla on a rocky bottom in 80 fathoms.

Distylia rugosa Moore

Distylia rugosa Moore (1904), p. 499, pl. 38, figs. 38-41.

Collected from San Pedro; several from an unknown locality.

Eudistylia polymorpha Johnson

Eudistylia polymorpha Johnson (1901), p. 429, pl. 17, figs. 179-183; pl. 8, figs. 184-185.

Collected from Ocean Cape and Yakutat Bay, Alaska; Puget Sound; Pacific Grove; and San Pedro.

Schizobranchia nobilis Bush

Schizobranchia nobilis Bush (1904), p. 207, pl. 24, fig. 3; pl. 28, fig. 7; pl. 33, fig. 22; pl. 35, figs. 1, 3-8, 10, 11, 23.

Collected from Orca in Prince William Sound, Alaska; and Port Townsend, Wash.

Family SERPULIDAE

Serpula columbiana Johnson

Serpula columbiana Johnson (1901), p. 432, pl. 19, figs. 199-204.

Collected from Puget Sound; Trinidad; Shelter Cove, Mendocino County; Bolinas; Duxbury Reef; Point Cavallo, San Francisco Bay; Pillar Point, California; Santa Monica; and San Diego.

Eupomatus uncinatus Philippi

Serpula uncinatus Philippi (1844), p. 195.

Collected from San Pedro and San Diego Bay.

Eupomatus gracilis Bush

Eupomatus gracilis Bush (1904), p. 234, pl. 27, fig. 9; pl. 34, fig. 25; pl. 37, figs. 26, 27.

Collected from San Pedro and San Diego.

Hydroides sp. (?)

A number of tubes marked "yacht bottom, Honolulu," were in the collection, and contained specimens of *Hydroides* too poorly preserved to admit of an examination of the soft parts. Collar setae are of two kinds. One (pl. 12, fig. 47) has a stout base, divided distally into three branches. Two of these are very short and stout while the other is a long slender process. None were entire, but apparently the end is rounded rather than pointed. The second kind of seta is long and slender, very gradually tapering to an acute tip with a narrow and much striated wing along one edge. The uncinus is of usual form and has six or seven teeth.

The basal plate of the operculum has thirty-two acute, conical, and sharp-pointed teeth around its edge. The terminal plate is very prominent and has thirteen arm-like expansions, each prolonged at its apex into a crescent-shaped expansion (pl. 12, fig. 48).

Apomatus geniculata Moore

Apomatus geniculata Moore (1904), p. 168, pl. 11, figs. 17, 18; pl. 12, fig. 38.

Collected in haul 1552, off San Clemente Island in 50 fathoms on coarse sand.

Protula atypha Bush

Protula atypha Bush (1904), p. 228, pl. 37, figs. 1, 2, 4.

Collected in the following hauls: XII-1, off San Pedro in 40 to 145 fathoms on green mud and sand; XXXV, off Ballast Point, Santa Catalina Island in 6 to 30 fathoms on green mud; LXXXII-1, off Point Firmin in 27 to 30 fathoms on fine gray sand.

Spirabbranchus quadricornis Grube

Spirabbranchus quadricornis Grube (1878), p. 275, pl. 15, fig. 6.

Collected from San Pedro; Avalon, Santa Catalina Island; La Jolla; and San Clemente Island.

Crucigera zygophora Johnson

Crucigera zygophora Johnson (1901), p. 433, pl. 19, figs. 205-208.

Collected from Sitka Harbor, Alaska; and Santa Barbara.

Crucigera websteri Benedict

Crucigera websteri Benedict (1886), p. 550, pl. 21, figs. 24-25; pl. 22, figs. 28-30.

Collected from San Pedro.

Family HERMELLIDAE

Sabellaria californica Fewkes

Sabellaria californica Fewkes (1889), p. 130, pl. 7, figs. 3-4.

Collected from Lime Point, San Francisco Bay; Pacific Grove; Santa Barbara; Deadman's Island, San Pedro; San Pedro; La Jolla; Point Loma, San Diego; and Coronado. Collected also in the following hauls: XLV, along the rocky shore of San Diego Bay; XLVI-2, off San Diego in 5 to 6 fathoms on sand; LXXXII-1, off Point Firmin in 27 to 30 fathoms on fine gray sand.

Sabellaria cementarium Moore

Sabellaria cementarium Moore (1906), p. 248, pl. 12, figs. 45-51.

Collected from Portuguese Bend; San Pedro; and San Diego. Collected also in the following hauls: XVI-2, off San Pedro in 9 fathoms on small rocks and pebbles; LXII, off San Diego in 16 to 18 fathoms on gray sand; LXVII, off San Diego in 19 to 31 fathoms on yellowish-gray sand; LXXXII-1, off Point Firmin in 27 to 30 fathoms on fine gray sand; 1166, off La Jolla on a sandy bottom in 5 to 13 fathoms.

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EXPLANATION OF PLATES

PLATE 11

Fig. 1. Head of *Panthalis pacifica*. $\times 15$. The terminal joint of one tentacular cirrus on the right side had been lost.

Fig. 2. First parapodium of *Panthalis pacifica*. $\times 23$.

Fig. 3. Eighth parapodium of *Panthalis pacifica*. $\times 23$.

Fig. 4. Terminal portion of seta from first parapodium of *Panthalis pacifica*. $\times 280$.

Fig. 5. Tip of ventrally placed seta from first parapodium of *Panthalis pacifica*. $\times 280$.

Fig. 6. Tip of very large seta from eighth parapodium of *Panthalis pacifica*. $\times 280$.

Fig. 7. Tip of dorsalmost seta from eighth parapodium of *Panthalis pacifica*. $\times 280$.

Fig. 8. Head of *Nereis notomacula*. $\times 20$.

Fig. 9. First parapodium of *Nereis notomacula*. $\times 45$.

Fig. 10. Eighth parapodium of *Nereis notomacula*. $\times 45$.

Fig. 11. Seta from eighth parapodium of *Nereis notomacula*. $\times 280$.

Fig. 12. Hooked seta from eighth parapodium of *Nereis notomacula*. $\times 280$.

Fig. 13. Ventral crochet and dorsal aciculum of *Leodice biannulata*. $\times 280$

Fig. 14. Head of *Spio acuta*. $\times 30$.

Fig. 15. First parapodium of *Spio acuta*. $\times 68$.

Fig. 16. Thirteenth parapodium of *Spio acuta*. $\times 45$.

Fig. 17. Seta of thirteenth parapodium of *Spio acuta*. $\times 185$.

Fig. 18. Parapodium from region of body behind twenty fifth somite of *Spio acuta*. $\times 45$.

Fig. 19. Seta from first parapodium of *Spio acuta*. $\times 185$.

Fig. 20. Hooded seta from first somite of *Spio acuta*. $\times 185$.

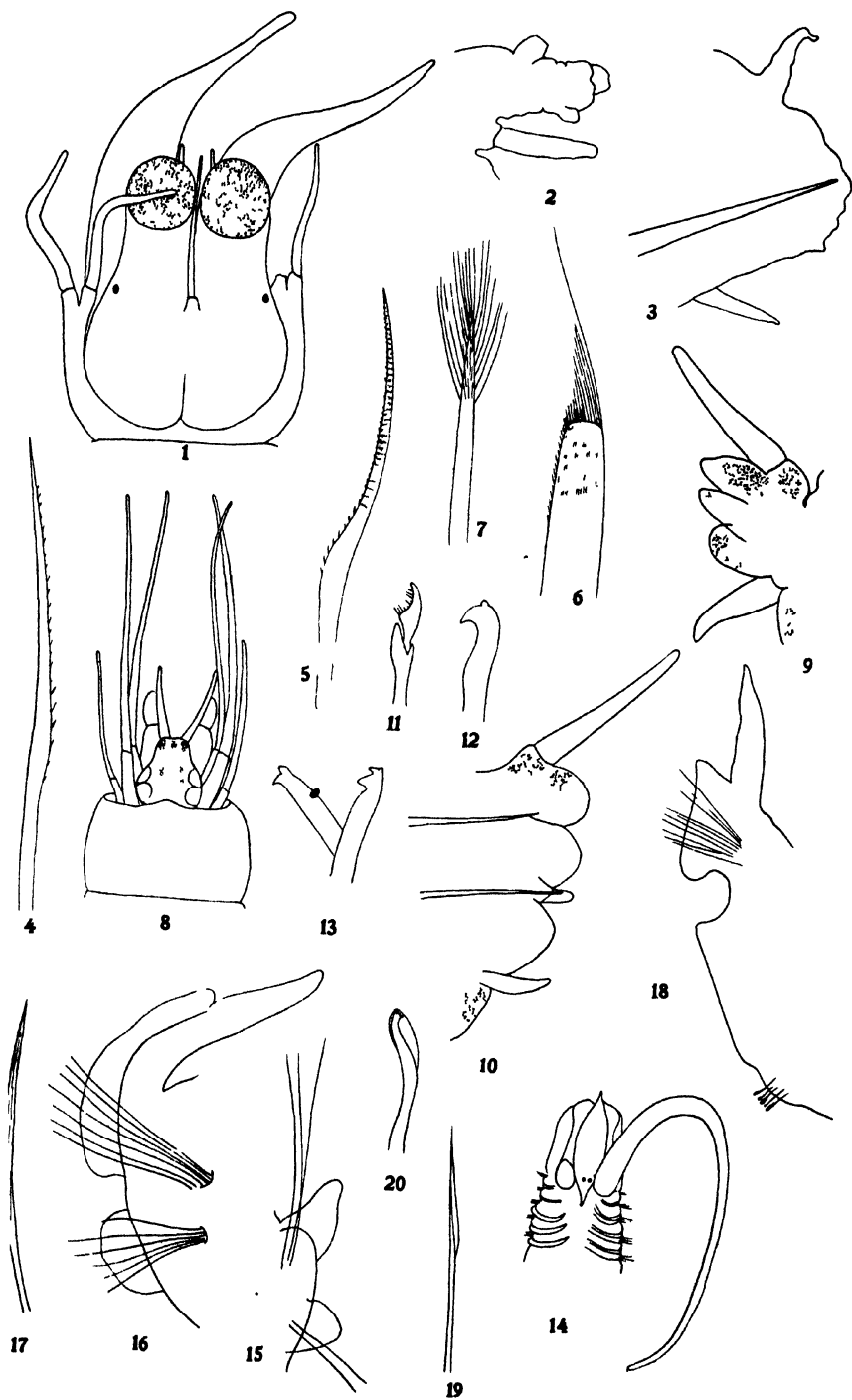
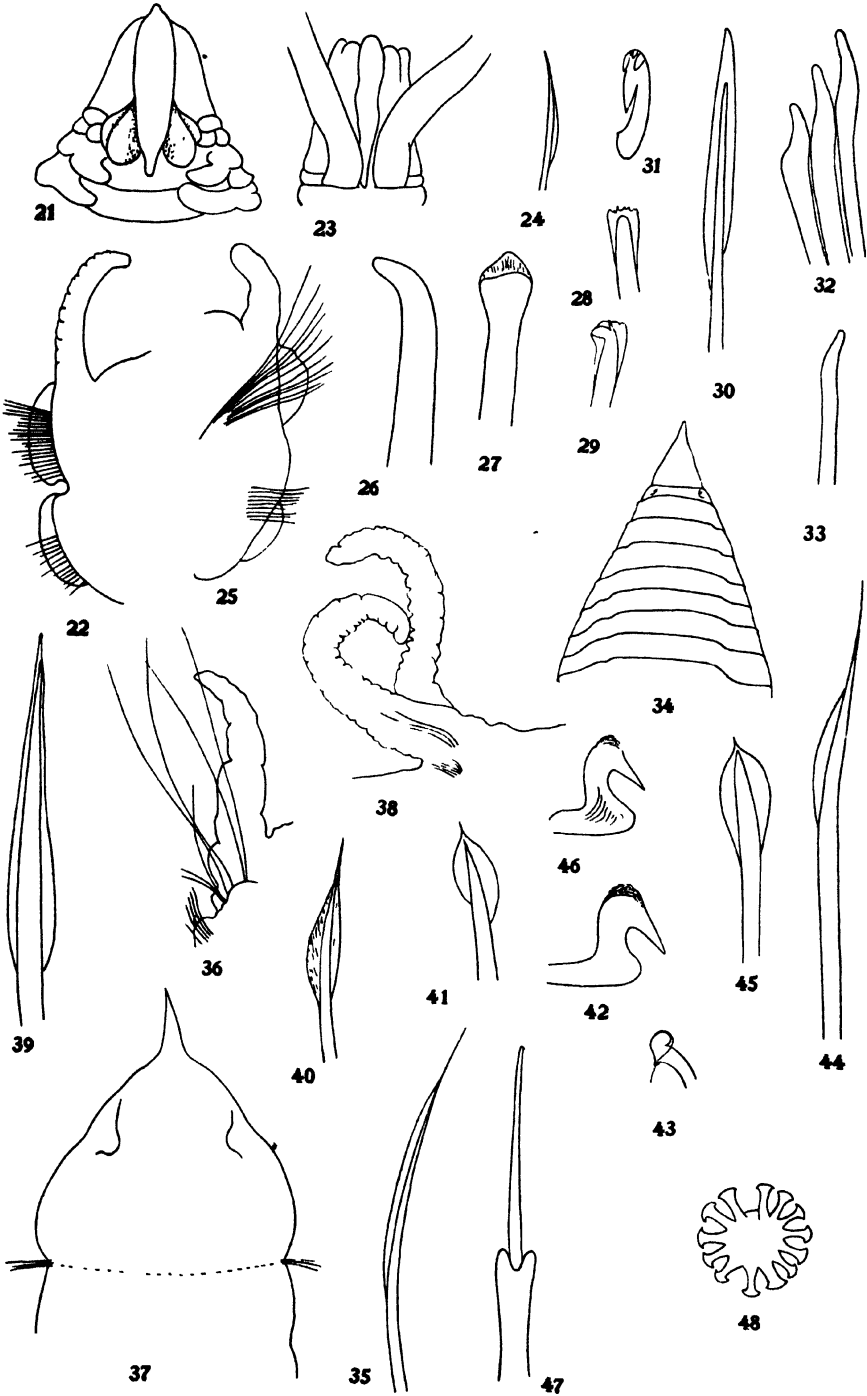


PLATE 12

- Fig. 21. Head of *Scolecoplepis alaskensis*. $\times 5$.
- Fig. 22. Parapodium from region of twenty fifth somite, of *Scolecoplepis alaskensis*. $\times 5$.
- Fig. 23. Head of *Polydora californica*. $\times 28$.
- Fig. 24. Seta from first neuropodium of *Polydora californica*. $\times 280$.
- Fig. 25. Third parapodium of *Polydora californica*. $\times 68$.
- Fig. 26. Hook from sixth somite of *Polydora californica*. $\times 185$.
- Fig. 27. Second form of hook from sixth somite of *Polydora californica*, $\times 185$.
- Figs. 28 and 29. Two views of a ventral hook from somite behind the sixth, of *Polydora californica*. $\times 185$.
- Fig. 30. Seta from fifth setigerous somite of *Streblosoma crassibranchiata*. $\times 280$.
- Fig. 31. Uncinus from *Streblosoma crassibranchiata*. $\times 560$.
- Fig. 32. Ventral hooks of *Trophonia minuta*. $\times 68$.
- Fig. 33. Notopodial hook of *Trophonia inflata*. $\times 68$.
- Fig. 34. Head of *Ophelina magna*. $\times 10$.
- Fig. 35. Seta from first setigerous somite of *Ophelina magna*. $\times 185$.
- Fig. 36. Fourteenth parapodium of *Ophelina magna*. $\times 14$.
- Fig. 37. Head of *Ophelina mucronata*. $\times 45$.
- Fig. 38. Gills of *Ophelina mucronata*. $\times 45$.
- Fig. 39. Dorsal collar seta of *Laonome oculifera*. $\times 185$.
- Fig. 40. Ventral collar seta of *Laonome oculifera*. $\times 185$.
- Fig. 41. Ventral thoracic seta of *Laonome oculifera*. $\times 185$.
- Fig. 42. Thoracic uncinus of *Laonome oculifera*. $\times 185$.
- Fig. 43. Pennoned seta from thorax of *Laonome oculifera*. $\times 185$.
- Fig. 44. Collar seta of *Branchiomma disparoculatum*. $\times 185$.
- Fig. 45. Spatulate thoracic seta of *Branchiomma disparoculatum*. $\times 185$.
- Fig. 46. Uncinus from thorax of *Branchiomma disparoculatum*. $\times 185$.
- Fig. 47. Collar seta of *Hydroides* sp. $\times 185$.
- Fig. 48. Terminal plate of operculum of *Hydroides* sp. $\times 8$.



NEW SYLLIDAE FROM SAN FRANCISCO BAY

COLLECTED BY THE U. S. S. "ALBATROSS"

BY

AARON L. TREADWELL

The two annelids here described were discovered in the collections submitted to me for identification which were made by the U. S. S. "Albatross" in conjunction with the Survey of San Francisco Bay, made jointly by the United States Bureau of Fisheries and the University of California. The paper is published by permission of the United States Commissioner of Fisheries.

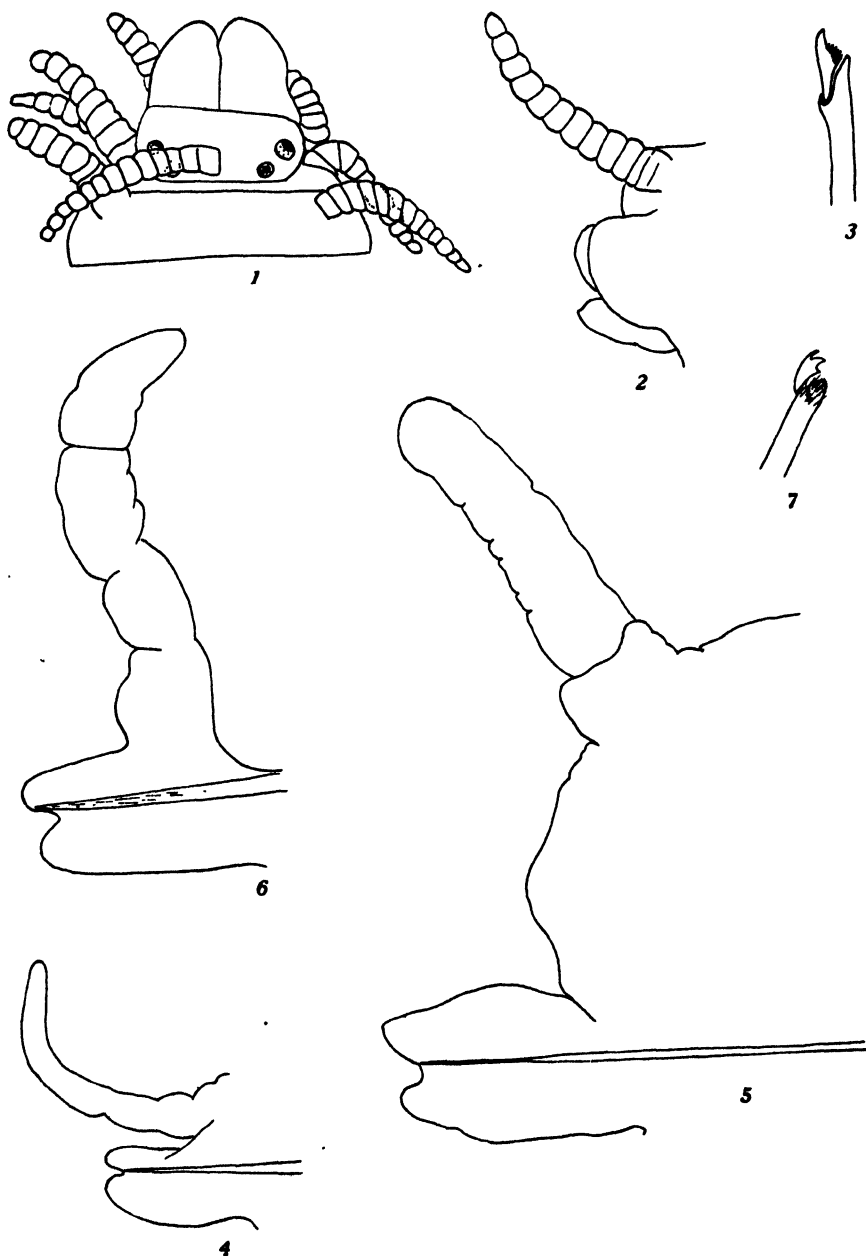
***Trypanosyllis adamanteus* sp. nov.**

Type a sexually mature female of 90 somites. Length 22 millimeters. Greatest width rather less than 2 millimeters.

Head (see fig. 1, from cotype), with width about 4 times length. Anterior and posterior edges parallel, the latter a trifle shorter than the former, sides decidedly convex. Palps 1.5 times the length of head, separate to their bases, but closely appressed along their median edges. Eyes, 2 pairs, about equal in size, brown, the posterior with its lens pointing dorsally, the anterior with its lens pointing antero-laterally. Paired tentacles with 9 or 10 joints, extending only to a short distance beyond palps. Median tentacle longer, with 13 joints.

Somite 1 very short dorsally, much longer ventrally, forming a posterior and 2 lateral lips to the mouth. Tentacular cirri with 9 to 12 joints, and much thicker on one side than on the other in the specimen figured. This was probably due to unequal pressure of the cover glass.

Somite 2 about 4 times as long as 1, widening noticeably from anterior to posterior border. Later somites are still wider, the full width of the animal being reached at about somite 20.



- Fig. 1. Head of *Trypanosyllis adamanteus*. $\times 60$.
 Fig. 2. Parapodium of *Trypanosyllis adamanteus*. $\times 60$.
 Fig. 3. Seta of *Trypanosyllis adamanteus*. $\times 280$.
 Fig. 4. Tenth parapodium of *Autolytus varius* sp. nov. (*Sacconereis*). $\times 60$.
 Fig. 5. Middle parapodium of *Autolytus varius* sp. nov. $\times 60$.
 Fig. 6. Posterior parapodium of *Autolytus varius* sp. nov. $\times 60$.
 Fig. 7. Seta of *Autolytus varius* sp. nov. $\times 280$.

Dorsal cirri of about 15 joints, indistinct at base, but much more distinct dorsally. Anal cirri 2, short, blunt, and not articulated. Parapodium (fig. 2), with rounded anterior and posterior lobes, the former a little longer than the latter, with a tuft of compound setae arising between them. Ventral cirrus beneath anterior lobe, apex not reaching to apex of lobe. Setae all alike, compound, basal joint relatively rather stout, slightly enlarged and obliquely truncated at apex. Terminal joint with large blunt, apical tooth, and a row of a few spine-like teeth along concave edge. These are much larger at the proximal than at the distal end (fig. 3).

At anterior end uniformly marked dorsally with numerous minute brown spots. At somite 2 a dorso-median clear area appears, which by somite 10 has formed a diamond-shaped patch in the center of the dorsal surface of each somite, surrounded by a dense patch of pigment granules. Usually a distinct line of these granules runs along the edge of the somite, anterior and posterior to the colorless area, ending in a triangular patch with its apex at the edge of the somite.

Oesophagus with about 10 broad blunt lobes, and a single large anterior tooth.

Type from Presidio shore, west of Fort Point, between tide marks. Co-type from Station D 5708, in dredge on sandy mud, at 10.5 to 12.75 fathoms.

***Autolytus varius* sp. nov. *Sacconereis* phase**

A single specimen, apparently not previously described from the Pacific coast. The body is divided into three regions. 1. Beginning with the head, with a diameter of 1 millimeter and extending to somite 15, with a diameter of approximately 2.5 millimeters. 2. The median region, carrying a brood sack, indicated by the prominent setae and by the brood sac filled with larvae. At somite 25 the body has a width of 3 millimeters. From somite 35 to somite 45 is a progressive narrowing, the latter somite marking the limit of the median region. 3. The posterior portion, having a fairly uniform diameter until at the very end it narrows to a blunt point.

Head with breadth about twice the length, with slight anterior median notch. Palps not visible from above, small, apparently separate but line of division not sharply indicated. Eyes two pairs, anterior very large, brown, with prominent lenses, when seen from anterior view making more than three quarters of the vertical diameter

of the head. Posterior eyes about one-quarter of the diameter of the anterior ones. Median and lateral tentacles about equal in size, length about 5 or 6 times that of head, faintly constricted at intervals but not regularly jointed, with granules of brownish pigment arranged in more or less of a segmental pattern along anterior faces of each. Tentacular cirri two pairs, dorsal ones one-quarter longer than antennae, and much stouter. Ventral ones slender, scarcely half the length and diameter of the dorsal.

First somite with dorsal cirrus larger than dorsal tentacular cirrus, later ones progressively smaller but after about somite 10 the size is uniform to the posterior end. All cirri marked with pigment in same manner as the antennae.

Anterior parapodia (fig. 4) with narrower dorsal and broader ventral lip, the latter postsetal. A single aciculum arises between the two. No distinct ventral cirrus. Dorsal cirrus more or less lobed but not articulated. Setae all compound with very short terminal joints.

Throughout median region the two setae lobes are nearly alike in size and form (fig. 5) and the tuft of compound setae arises between them. Dorsally, from the end of an inconspicuous squarely truncate notopodium arises a tuft of long natatory setae, in length equal to the transverse diameter of the body. Each has a parallel-sided, flat basal portion sharply ruled by parallel longitudinal lines. This portion widens toward the end to about twice its original diameter, becoming at the same time very much thinner. None was entire at the tip, but apparently they end in a sharp point. A large aciculum extends into the notopodium, and surrounding it, but not penetrating the surface, is a tuft of about 15 long, slender, curved needle-like setae. Compound setae are similar in form to those in the anterior region, but do not protrude quite so far from the surface. Dorsal cirrus relatively much shorter than anteriorly.

Posterior parapodia (fig. 6) in general form like the anterior ones, but with larger dorsal cirrus which may show an indication of jointing. Compound setae small, basal portion expanded at end and covered with minute spines. Terminal portion with two sharp teeth (fig. 7).

Collected at Bonito Point, near the outer end of the entrance to San Francisco Bay.

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NOTE ON THE MEDUSAN GENUS
STOMOLOPHUS, FROM SAN DIEGO

BY

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The following note is prompted by the receipt of several specimens of *Stomolophus*, from San Diego Bay, California, where this medusa was abundant during August and September, 1913, which differ strikingly in color from their Atlantic ally, *Stomolophus meleagris* L. Agassiz. In the latter, which often swarms off the coasts of the Carolinas, the gelatinous substance of the bell is bluish or yellowish, the entodermal parts dull yellow, the exumbrella reticulated with brown pigment, and its marginal zone thickly set with whitish or yellowish dots. For an excellent account of *S. meleagris*, see Mayer (1910, p. 710). In the San Diego specimens the general color of the bell is Prussian blue, pale at the apex, deeper at the margin; the exumbrella is speckled with deep Prussian blue spots, which are most numerous and largest near the margin, progressively fewer and smaller towards the apex; but not altogether absent from any definite part of the disc. Dissection shows that these dots are not on the surface, but lie imbedded in the gelatinous substance of the bell, the largest ones deepest. The oral arms are likewise pale Prussian blue; the lips whitish.

But striking as is the color difference between the San Diego and the Atlantic representatives of *Stomolophus*, it is not accompanied by any structural differences which would warrant separating the former, specifically, from the latter. Up to the present time four "species" of *Stomolophus* have been described, viz.: *meleagris* L. Agassiz, from the South Atlantic Coast of the United States to South America; *fritillaria* Haeckel, from the North Coast of South America (Surinam); *agaricus* Haeckel, from the Pacific coast of Central America

(Costa Rica); *chuni* Vanhöffen, from the Gulf of Panama. And the genus *Brachiolophus* of Haeckel is nothing but the young of *Stomolophus*, as pointed out by Mayer (1910). The relationships of these four supposed species to one another have been discussed by Mayer (1910); and I think there is no escape from his conclusion that of the various characters which have been supposed to separate them, the only one which is anything more than an evidence of contraction, or of varying stages in development, is the number of lappets per octant of the margin. According to the published accounts, *meleagris* has 16, *fritillaria* about 26, *chuni* 14, and *agaricus* 20. Mayer unites *chuni* and *meleagris*, saying, no doubt correctly, that the former is merely a younger stage of the latter; but retains *fritillaria* as a recognizable variety. However, the following counts of the lappets in specimens from South Carolina and Cuba show that there is no discontinuity between *meleagris* with 16 and *fritillaria* with 26:

Locality	Diameter in mm.	Lappets per octant
South Carolina	85	19 in one octant
Cuba	150	19, 20, 22, 21
San Diego	100	22 in one octant

Unfortunately, it seems to be rare to find an entire octant undamaged, even in specimens in good condition otherwise. But this is enough to show that there is no correlation between number of lappets and geographic occurrence. And it shows, further, that large specimens from the southeast coast of the United States may have a considerably greater number of lappets than they have usually been credited with. In short, there is no longer any reason to retain *fritillaria* as distinct from *meleagris* even as a variety, or to separate the San Diego or Panama specimens from the latter. All forms of *Stomolophus* which have yet been described must be grouped together as one species, *S. meleagris*.

Whether the two color varieties of this species are constant, or whether they vary, or intergrade, is yet to be determined; unfortunately, Vanhöffen's (1888) specimens from Panama, Haeckel's (1880) material, and the South American specimens recently described by Trinci (1906) were all alcoholic, and consequently must have lost whatever color characterized them in life. But even if the color phases are distinct, the phenomenon is not unparalleled, though unusual, among medusae, a striking example of the same sort being afforded by *Cassiopea xamachana* (Mayer, 1910, p. 643).

From the zoogeographical standpoint the demonstration that the same species of *Stomolophus* occurs both in the Pacific and Atlantic, but limited to American waters of comparatively high temperature in both, and the fact that this genus is unknown elsewhere, is of considerable interest as adding another instance to the list of littoral Medusae which are found on both sides of temperate and Central America; a phenomenon which I have discussed elsewhere (1909, p. 227). Hence Mayer (1910, p. 711) is justified in saying that *S. meleagris* has remained unchanged since the closure of the Isthmus in Mesozoic times.

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April 17, 1916

A STUDY OF THE STRUCTURE OF FEATHERS,
WITH REFERENCE TO THEIR TAXO-
NOMIC SIGNIFICANCE

BY
ASA C. CHANDLER

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INTRODUCTION

I. OBJECT AND SCOPE OF PAPER

Although as a class birds have received more attention from nearly all classes of zoologists than any other group of vertebrate animals, their natural classification presents a great many problems difficult of solution, and no satisfactory phylogenetic arrangement has yet been devised for them. It was with the hope of throwing light on some of the dark places in the taxonomy of birds that the writer attempted the work, the results of which are presented in this

paper, since it was believed that the comparative morphology of feathers would almost certainly be of some taxonomic value in establishing the relationships of various groups of birds.

Since feathers are external and in constant contact with the environment, they would naturally be expected to be among the first structures of the body to feel the influence of environmental changes and shocks, and would still be as liable to change by hybridization, orthogenesis or any other method of evolution, as any of the other structures.

There are numerous groups of birds, the taxonomic position and phylogenetic relationships of which have been in very great doubt. As far as possible the feathers of these groups have been studied with the hope that the structure of the feathers would reveal relationships that the structure of the other organs would not, on account of parallel adaptations in the latter. Instances in which the morphology of feathers has been found in this study to throw light on doubtful relationships are numerous, for example, in the case of the Phoenicopter, Tinamidae, and Pici.

Provided that birds were found to possess constant and peculiar characters in the structure of their feathers, the results of such work would be of high economic importance in the identification of feathers used commercially, and for the confiscation of feathers illegally used in commerce. This belief, in the course of the work, has been amply justified, and already successful diagnoses of unknown feathers have been made for the United States Customs officers in the port of San Francisco.

Before undertaking a study of the phylogenetic modifications in feathers, a careful study was made of the structural modifications of feathers in the different parts of the plumage of a single representative bird, namely, *Circus hudsonius* (Chandler, 1914). It was discovered that certain general modifications found in this bird in the structure, not only of different feathers, but of different parts of the same feather, occur almost uniformly throughout the class. A discussion of the typical structure of various kinds of feathers, with a consideration of the more important modifications of structure correlated with color production, constitutes the first part of this paper, while the second part deals with special group characters, modifications and peculiarities, arranged in systematic order. No attempt has been made to make a systematic study of the morphology of any feathers except those of adult birds—i. e., of teleoptiles.

II. ACKNOWLEDGMENTS

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Other material was procured from the Memorial Museum in Golden Gate Park, San Francisco, through Mr. W. G. Blunt of the Natural History department. The writer is further indebted to the California Academy of Sciences in San Francisco, for the use of its collection of water birds, and to the Bentley Ostrich Farm of Oakland, California, for the supply of ostrich feathers, and assistance in the examination of living birds.

III. HISTORICAL

The first thorough and reliable work on feathers was done by Nitzsch, a German ornithologist. This work was edited and published by Burmeister, and later translated into English and published in the *Transactions* of the Ray Society in 1876, a few of the misconceptions of the original author being rectified in the process.

This work, though dealing primarily with pterylography, contains the first approximately accurate account of the structure of feathers to be found in the whole literature of the subject, and may justly stand as a masterpiece. Following Nitzsch, a number of works on the development and structure of feathers appeared, among which may be mentioned especially Clement (1876), Studer (1878), Jeffries (1884), Klee (1886), Davies (1889), and Strong (1902); and, more particularly on structure, Wray (1887b), Pycraft (1893), and Mascha (1904). Many other less general but highly valuable papers

on the structure and development of feathers have appeared, but need not be mentioned here.

Throughout the literature, no general attempt has been made to use differences in the morphology of the minute structures of feathers as taxonomic or diagnostic characters. In a few cases where feathers differ macroscopically and obviously from the usual type, as in cassowaries and penguins, they have been considered as of taxonomic value, and the presence or absence, or degree of development, of the aftershaft has been so used. Jeffries (1884) realized that differences in the microscopic structures of feathers existed in different groups of birds, as shown by the following quotation from the paper cited: "The minute structures of these (wing and tail feathers) vary in different groups of birds, as I have myself observed, and has, I believe, been pointed out by Schroeder, though I have not seen his paper." In Newton's *Dictionary of Birds*, under the article on "Feather", is a similar statement as follows: "Cilia which are not furnished with hooks frequently have shapes which may possibly prove to be characteristic of different groups of birds".

The only actual investigation of group differences in the microscopic structure of feathers was done by Mascha (1904). His work is accurate and suggestive as far as it goes, but he dealt only with the remiges of a very limited number of species, and, as would be expected from such a restricted survey, he missed entirely the taxonomic value of certain of the most characteristic features in the microscopic structure of feathers, and contributed but little towards our knowledge of the systematic and phylogenetic value of feather structures.

In recent years considerable work has been done by zoologists in the study of the morphology and the taxonomic value of other integumentary structures of vertebrates, and their results point to the fact that such structures, though constantly in contact with the environment, and subject to more external influences than any other organs of the body, nevertheless possess phylogenetic characters which are remarkably constant and easily recognizable.

The work of Toldt (1912) on the hair of mammals, like Mascha's (1904) work on feathers, though only a beginning, is careful and accurate as far as it goes, and is highly suggestive in that it points the way to a field which is still almost untouched. Work along similar lines on the scales of reptiles has been done by Stehli (1910). His study was rather a general treatise on a few types, designed

in part to show the relation of the scalation to the segmentation of the musculature, but his description and figures indicate that modifications of taxonomic value undoubtedly exist in the scales of reptiles. The scales of fishes have received more attention than any of the structures in other groups which in a general way are analogous, and these are the only integumentary growths, the morphologic modifications of which have heretofore been actually applied to taxonomic and phylogenetic problems. A series of papers by T. D. A. Cockerell (1909-1913) deals with the actual taxonomic application of scale structures, and gives keys to families and genera based on these characters. Cockerell (1911c and 1912) has shown that the scales of coeciliids also show characters which are of value in classification.

In view of the fact that all these integumentary structures of vertebrates are homologous, or at least in a general way analogous, to each other, and that investigations of them, in a general way, present similar problems, and are governed by the same limitations, and in fact frequently overlap each other, it seems to the writer that a common name should be applied to the study of them. For this study, which shall include the study of the development, morphology, and phylogenesis of vertebrate scales, hair, and feathers, and any other homologous or analogous structures, the writer wishes to suggest the name *Epiphylogy* (based upon ἐπιφύειν, to grow upon) as a general term for the "study of outgrowths". In creating this term it is admitted that the formation is not perfectly valid etymologically.

IV. NOMENCLATURE AND DEFINITIONS

It is unfortunate that in the literature of feathers there has been a very notable lack of uniformity in the use and meaning of terms, resulting in no little confusion and inconvenience, considerably more so among German writers, however, than among others. After a careful study of the history and usage of the nomenclature of feathers, the writer has selected a terminology which, taking all points of view into consideration, seems to be the most logical and widely applicable. These terms have been selected with regard (1) to the general usage, (2) to convenience, (3) to priority. It seems advisable to give a list of the terms here used to describe feathers, with their definitions, and in the case of terms which have been used inaccurately, the names of some of the authors who have used them in the sense here accepted. The more important synonyms are also given,

with their chief adherents in the case of terms not commonly used as alternatives. In a few cases new terms had to be coined, or old ones re-defined, but it is hoped that the terminology here used will meet with the approval of other workers, and come into general

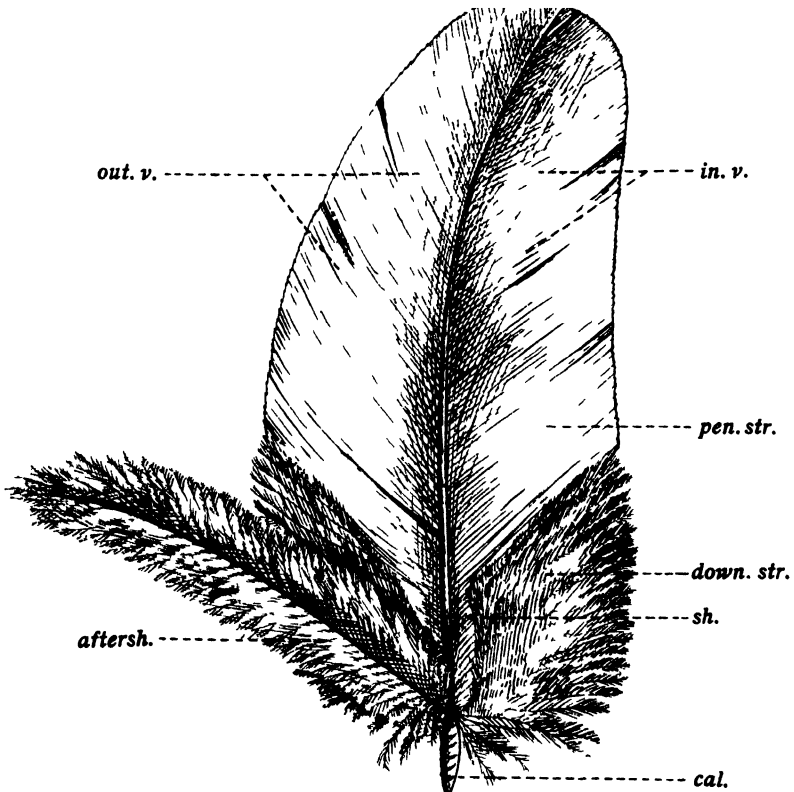


Fig. A. Typical contour feather. Abbreviations: *aftersh.*, aftershaft; *cal.*, calamus, *down. str.*, downy structure; *in. v.*, inner vane; *out. v.*, outer vane; *pen. str.*, pennaceous structure; *sh.*, shaft.

use, a thing which would go a long way towards establishing simplicity and clearness in the description of feathers and their structures. The terminology suggested is as follows:

TERMS OF ORIENTATION. In speaking of a feather, or any of its structures, "dorsal" and "ventral" are used as intrinsic terms, i. e., with reference to the feather itself, regardless of its position on the bird, dorsal meaning, therefore, the side of the feather which is usually exposed, or that opposite the superior umbilicus, which is considered to be upon the ventral side. Lateral is used with reference to the dorso-

ventral lines as here defined. Inner and outer, as applied to vanes, are used to mean respectively the vanes adjacent to and away from the next overlapping feather. Proximal and distal, as applied to entire barbules or vanules, refer respectively to those on the side of the ramus nearer to and away from the base of the feather. In all other cases, proximal and distal are used intrinsically with reference to the structure to which they apply; for example, the proximal part of a barb is the less remote, and the distal part the more remote, from the junction with the shaft. Inner and basal are sometimes used synonymously with proximal, while outer and terminal are likewise used in place of distal.

CONTOUR FEATHERS (fig. A). The feathers which form the contour of a bird's body, growing only in the pterylae, and always with well-developed shafts and calami. Eyelashes, ear-coverts, etc., and the semi-plumes of Nitzsch (1867) are considered as modified contour feathers. *German synonym*: Konturfedern.

PLUMULES. Small, downy feathers, more or less concealed, and with shaft never highly developed. They grow either in the apteria or pterylae, or both, often arranged in a definite manner around the contour feathers; absent in some birds (Nitzsch, 1867; Coues, 1884; Evans, 1899, *et al.*). *Synonym*: down or down feathers, a term for plumules which is objectionable on account of its loose application not only to plumules, but to any feather or part of feather possessing downy structure. *German synonyms*: Dunen (Gadow, 1891); Flaumfedern (Wiedersheim, 1909).

FILOPLUMES. Degenerate, hairlike feathers growing at the base of contour feathers, composed of a slender quill not differentiated into shaft and calamus, and much reduced vanes, the latter usually consisting of only a few barbs and barbules at the extreme tip. *German synonyms*: Haarfedern, Fadenfedern.

DOWN, or DOWNY STRUCTURE (fig. A). That type of feather structure which is produced by elongated, filamentous barbules, as opposed to a pennaceous structure (fig. A), which is produced by differentiated distal and proximal barbules or modifications of them, i. e., pennaceous barbules, as here used. *German synonym*: Dunen.

QUILL (fig. A). The main stem of a feather, including both shaft and calamus (Coues, 1884; Beebe, 1906, *et al.*). *Synonyms*: main stem (Nitzsch, 1867), scapus (Nitzsch, 1867; Sundevall, 1886; Pycraft, 1893), primary quill (Mascha, 1905). *German synonyms*: Kiel (Gadow, 1891), Hauptkiel (Mascha, 1904).

CALAMUS (fig. A). The hollow basal portion of the quill, proximal to the superior umbilicus. *Synonym*: barrel (Newton, 1899), tube (Nitzsch, 1867). *German synonym*: Spule, of general use.

INFERIOR UMBILICUS. The proximal end of the calamus, where the papilla finally closes after the maturity of the feather.

SUPERIOR UMBILICUS. The pore at the distal end of the calamus, at the junction of shaft and aftershaft, or, in some feathers, where the inner and outer vanes meet. *Synonym*: umbiliciform pit (Nitzsch, 1867; Newton, 1899). *German synonym*: Nabel (Gadow, 1891).

SHAFT (fig. A). The portion of the quill distal to the superior umbilicus upon which are borne the vanes. *Synonyms*: rhachis, used generally as an alternative in heavier scientific writing. *German synonym*: Schaft, of general use.

AFTERSHAFT (fig. A). The ventral counterpart of the shaft plus its vanes ("plate", see below), springing from the ventral lip of the superior umbilicus, sometimes vestigial or absent. *Synonyms*: hyporhachis, used as is rhachis for shaft; accessory plume (Sundevall, 1886). *German synonyms*: Afterschaft, Nebenschaft (Gadow, 1891); Afterfeder (Studer, 1878), Afterschaft, only its shaft (Studer, 1878).

PLATE. A convenient term used by Mascha (1905), to designate the shaft with both its vanes. *Synonym*: vexillum (Clement, 1876). *German synonym*: Flache (Mascha, 1904).

VANE (fig. A). That portion of the feather borne on one side of the shaft, composed of barbs, usually with barbules. Inner vane, that which is overlapped by the outer vane of the adjacent feather. *Synonym*: vexillum, web, common alternatives (the vexillum of Clement, 1876, equals plate), pogonium (Sundevall, 1886). *German synonym*: Fahne, of general use.

BARB (fig. B). A ramus or primary branch of the shaft plus its barbules (Beebe, 1906; Headley, 1895, *et al.*); has been loosely used by many authors to designate either the ramus alone, or the ramus with its barbules. *German synonyms*: words used for ramus also loosely used for barb; also Fiedern erster Ordnung (Haecker, 1896); Fiedern (Ahlborn, 1896).

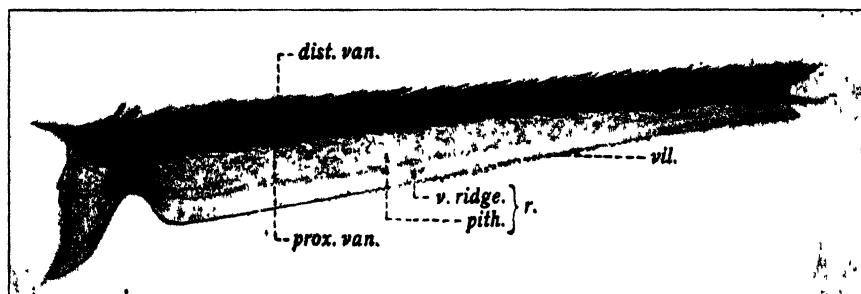


Fig. B. Proximal half of barb of duck. Abbreviations: *dist. v.*, distal vanule; *prox. van.*, proximal vanule; *r.*, ramus; *vll.*, villi.

RAMUS (figs. B and C). A primary branch of the shaft, forming the main stem or lamella of a barb, upon which are normally borne barbules. *Synonym*: barb (see above); secondary quill (Mascha, 1905). *German synonyms*: Aeste (Nitzsch, 1867; Gadow, 1891; Wiedersheim, 1909); Strahlen (Studer, 1878; Davies, 1889); Fiederlamelle (Ahlborn, 1896); Fäsern (Cuvier, 1809); sekundäre Kiele (Mascha, 1904).

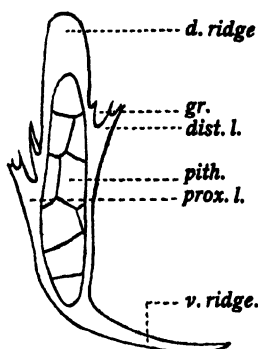


FIG. C

Fig. C. Cross-section of hypothetical barb. Abbreviations: *dist. l.*, distal ledge; *d. ridge*, dorsal ridge; *gr.*, groove for insertion of distal barbule; *prox. l.*, proximal ledge; *v. ridge*, ventral ridge.

VENTRAL RIDGE (figs. B and C). A horny keel on the ventral side of the ramus, usually narrow, though sometimes very highly developed (Strong, 1902; Mascha, 1905). *German synonym*: Hornleiste (Mascha, 1904).

LEDGE (fig. C). Longitudinal grooved ledges on the lateral sides of some rami, into which the barbules fit and which tend to hold them in place. Indefinitely called "ridges" or "longitudinal ridges" by Mascha (1905). *German synonym*: Gesims (Mascha, 1904).

BARBULE (figs. D, E and F). A branch of a ramus, collectively forming the vanules. Pennaceous barbules are those which are differentiated into a proximal and distal series which interlock by means of hooklets, unless the structure has been secondarily simplified. The proximal barbules (fig. D) are those which are borne on the side of the ramus nearest the base of the feather. The distal barbules (fig. E) those which are borne on the side nearest the tip. Downy barbules (fig. F) are those which are relatively long and filamentous, with no interlocking device. *Synonym*: radius, a common alternative; tertiary fibers (Mascha, 1905); hook fibers (= distal barbules) and curved fibers (= proximal barbules) (Mascha, 1904). *German synonyms*: Strahlen (Nitzsch, 1867; Gadow, 1891; Wiedersheim; sekundäre Strahlen (Studer, 1878); Fiederchen (Ahlborn, 1896); tertiäre Fasern (Mascha, 1904); Hakenfasern (= distal barbules) and Bogenfasern (= proximal barbules) (Mascha, 1904).

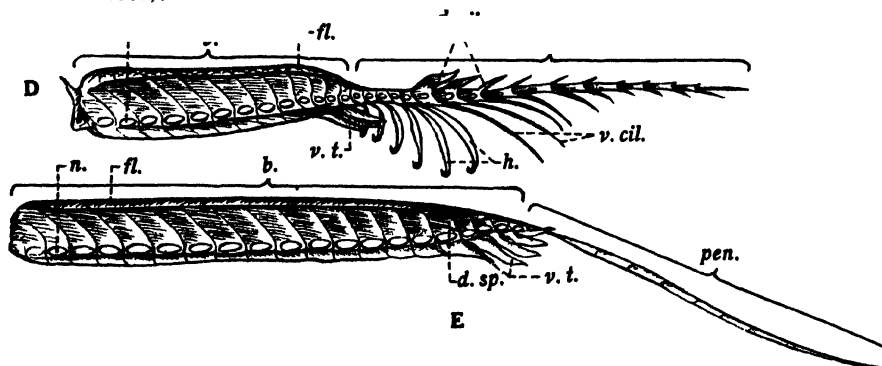


Fig. D. Diagrammatic distal barbule. Abbreviations: *b.*, base; *d. cil.*, dorsal cilia; *fl.*, flange; *h.*, hooklets; *n.*, nucleus; *pen.*, pennulum; *v. cil.*, ventral cilia; *v. t.*, ventral teeth.

Fig. E. Diagrammatic proximal barbule. Abbreviations: *b.*, base; *d. sp.*, dorsal spines; *fl.*, flange; *n.*, nucleus; *pen.*, pennulum; *v. t.*, ventral teeth.

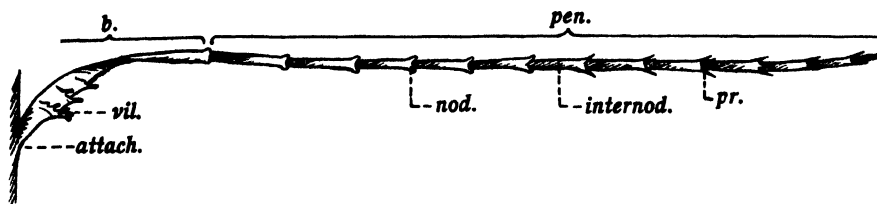


Fig. F. Diagrammatic downy barbule. Abbreviations: *attach.*, attachment with barb; *b.*, base; *internod.*, internode; *nod.*, node; *pen.*, pennulum; *pr.*, prongs; *vil.*, villi.

VANULE (fig. B). A new term here used to designate collectively all the barbules of either the distal or the proximal series, bearing the same relation to the barb that the vane bears to the feather plate. Hitherto referred to only as the "vane" of the barb.

BASE (figs. D, E and F). The proximal portion of a barbule, which is more or less lamelliform; in distal barbules the portion proximal to the hooklet cells, in proximal barbules the portion proximal to the bend occurring just beyond the ventral teeth, and in down barbules the short flattened portion at the junction with the ramus. *Synonym*: lamella (Newton, 1899). Otherwise referred to only by descriptive phrases. *German synonym*: Anfangstell (Mascha, 1904).

PENNULUM (figs. D, E and F). A new term here used to designate the more or less attenuated distal portion of a barbule, bearing the hooklets and cilia, or, in the case of down, the nodes. *Synonym*: tip (Chandler, 1914). Otherwise referred to only by descriptive phrases. *German synonym*: Endteil (Mascha, 1904).

FLANGE (fig. D and E). The thickened dorsal edge of the bases of pennaceous barbules, generally recurved in proximal barbules, and frequently so in distal barbules also (Wray, 1887). *Synonym*: recurved margin (Strong, 1902), and other descriptive phrases. *German synonym*: Rinne (Mascha, 1904).

DORSAL SPINES (fig. E). Recurved spines on the flange of proximal barbules, opposite the ventral teeth. *Synonym*: toothlike processes (Mascha, 1905). *German synonym*: Zahnforsätze (Mascha, 1904).

BARBICELS (figs. D and E). Outgrowths of the cells of the linear series forming pennaceous barbules, usually projections from the anterior dorsal or ventral corners of the cells. Used by Nitzsch (1867) and Pycraft (1893) to designate cilia only, but more commonly used in the broader sense here accepted. *Synonym*: cilia (sometimes used in this broad sense). *German synonyms*: Häkchen, Wimpern, of general use.

HOOKLETS (fig. D). Ventral barbicels which are strongly hooked at the tip, occurring only on the proximal portion of the pennulum of distal barbules. Hooklet-bearing cells never possess dorsal barbicels. *German synonym*: Häkchen, (Gadow, 1891; Nitzsch, 1867); Haken (Mascha, 1904).

CILIA (fig. D). Pennular barbicels, dorsal or ventral, occurring on distal barbules distal to the hooklets, and often on proximal barbules of the outer vane of highly developed feathers. *German synonym*: Wimpern (Nitzsch, 1867; Mascha, 1904); Häkchen (Studer, 1878).

VENTRAL TEETH (figs. D and E). Anteriorly projecting, ventral, basilar barbicels of both distal and proximal barbules of nearly all birds, often lobate or leaflike in distal barbules, usually toothlike in proximal barbules. *Synonym*: toothlike processes (Wray, 1887); ventral lobes (Mascha, 1905). *German synonym*: ventrale Lappen (Mascha, 1904).

FLEXULES (pl. 17, fig. 10e). A new term used to designate the curved barbicels occurring on the dorsal edge of the bases of distal and proximal barbules of the trunk feathers in some groups of birds (see p. 272). Hitherto apparently unknown.

NODES (fig. F). The junction of the cells of the pennulum of down barbules, usually characterized by swellings or outgrowths of some sort.

PRONGS (fig. F). Short, spiny outgrowths at the nodes of the down of many birds, differing from other barbicels in that three or more may occur on the distal end of a single cell, whereas there are never more than two cilia or other kinds of barbicels on a single cell.

V. METHODS

After experimenting with various methods of preparing feathers for microscopic study, especially the barbules, it was found that in most cases the examination of dry mounts of barbs and barbules gave entirely satisfactory results. This was at the same time so simple, and took so little time in preparation, that it was possible to examine the microscopic structures of the feathers of a very large series of birds, and thereby to determine with considerable precision the constancy and uniformity of characters in various groups.

The barbs were first studied under the microscope with their vanules intact. The vanules were then spread backward in order to separate the barbules for individual study, this being done by merely drawing the barb, tip first, between the thumb and forefinger. With a scalpel some of the barbules from each vanule were scraped off from the region of the barbule which it was desired to study, and mounted dry under a cover glass. In this way a considerable number of individual barbules could be separated, and as they would lie in all sorts of positions, their general form could be studied readily from such a preparation. The morphology of heavily pigmented structures could be studied more easily when mounted in balsam. In some cases also barbules were mounted in balsam in order to determine whether certain appearances were due merely to pigmentation, or to structural modification, and to determine the effect of oils of low refractive index on color-producing mechanisms. The methods of treating individual birds and groups of birds to determine their *epiphylogenic* characters will be discussed at the beginning of Part II.

PART I

GENERAL MORPHOLOGY

I. PLUMULES

1. *Unspecialized Plumules*

a) Occurrence and Distribution.—As remarked above, from a general survey of the feathers of a large number of species of birds, it is evident that certain generalizations regarding feather structures may be made. It is the intention of this portion of the paper to describe the general characters of various kinds of feathers, and to discuss briefly the range of modifications exhibited by them and their several parts.

Plumules are small downy feathers which are usually completely covered by the contour feathers in adult birds. Their distribution on the body differs a great deal in different kinds of birds. They may be (1) evenly distributed over the whole body, both in the apteria, and in the pterylae between the contour feathers; (2) sparsely or unevenly scattered over the whole body; (3) confined to the apteria; (4) confined to the pterylae (only in Tinamidae); or (5) absent entirely. The table on page 256 shows the nature of the distribution of plumules in the various groups of birds, the data being derived from Gadow (1891), Beddard (1898), and others.

In looking over this table it seems evident that a uniform distribution of plumules is to be considered a primitive condition, yet in all of the ratite birds, which have usually been considered the most primitive, they are absent entirely. It seems to me that this may be explained in one of two ways: either that the ratite birds have degenerated from a higher type and have lost their plumules concomitant with a simplification of their contour feathers from a pennaceous to a downy type, or that the ratite birds show a condition of plumage more primitive than any other birds, and that in the course of evolution the downy contour feathers of these birds developed along two separate lines, one leading to the soft, fluffy, almost shaftless plumules in both pterylae and apteria, the other to the highly specialized contour feathers in the pterylae only. Further

DISTRIBUTION OF PLUMULES

Group	Uniform and evenly distributed	Uniform but sparse	Apteria only	Absent or sparse in apteria	Pterygiae only	Aftershaft
Struthioniformes	+	-
Rheiformes	+	-
Casuariiformes	+	+, very large
Crypturiformes	+	-, or rudimentary
Apterygiformes	+	-
Sphenisciformes	+	+
Colymbiformes	+	+
Procellariiformes	+	+, rudimentary in <i>Diomedea</i>
Ciconiiformes						
Steganopodes	+	+, or rudimentary
Ardeae	+	+
Ciconiae	+	variable
Phoenicopteridae	+	+, well-developed
Anseriformes	+	-, rudimentary in a few genera
Falconiformes	+	+, - in <i>Pandion</i> and <i>Cathartidae</i>
Galliformes	+	+, large or small
Opisthocomi	+	+
Mesaenatides	+(?)	-
Gruiformes	+ or +	variable, usually present
Charadriiformes						
Larolimicolae						
Alcidae	+	+
Others	+	+
Pteroclo-Columbae	+	small or rudimentary
Cuculiformes						
Psittaci	+	+, large
Cuculi	+	-, or rudimentary
Coraciiformes						
Coraciidae	+	
Alcedinidae	+	-
All others	+	+, often rudimentary
Strigidae	+	-, rudimentary in <i>Aluco</i>
Caprimulgi	+	small or -
Micropodii	+	+
Trochilidae	+	+
Coli and Trogonidae	+	+
Passeriformes and						
Pici	+	+, not highly developed

evolution, if this hypothesis be true, resulted in the segregation of contour feathers into tracts, and the reduction of plumules, first between the contour feathers, and finally on the whole body, culmi-

nating in the condition found in passerine birds and allied forms. There is further evidence in support of the latter alternative in that, so far as I have been able to discover, filoplumes also are totally absent in the Ratitae, while, so far as is known, they are present, associated with contour feathers, in all other groups of birds.

b) *Structure*.—In general structure plumules are remarkably constant, not only on different parts of the body, but also throughout the entire class of birds. On different parts of the body of an individual the only appreciable modification is in size, the plumules of the larger apteria usually being the largest.

The quill in plumules is invariably short and inconspicuous. The calamus, which is hollow and barrel-shaped, having a more or less inflated appearance, is usually entirely imbedded in the skin. The shaft is always short and poorly developed, very soon breaking up entirely into barbs in a more or less fan-shaped manner, and it is plainly evident, in the majority of cases, that the thin, flat, more or less subtriangular shaft is to be looked upon merely as a basal coalescence of the barbs. The plumules possess an aftershaft in groups which are characterized by the presence of an aftershaft in the contour feathers, even if only rudimentary in the latter. Since many of the birds which lack an aftershaft are also devoid of plumules, it is rare to find the latter with a single shaft. Owls, which lack an aftershaft on the contour feathers, with the exception of a rudimentary one in *Aluco*, have plumules with only one shaft, a dense cluster of barbs springing from the sides and ventral lips of the superior umbilicus. *Pelecanus* was stated by Nitzsch (1867), and restated by other authors, to have plumules with no shafts. This is not strictly true. *Pelecanus erythrorhynchus* has plumules with two fairly well-developed shafts, equivalent to each other, about 1.6 mm. long, which possess a brown pigment, the rest of the plumule being unpigmented. In *Phalacrocorax* (*P. penicillatus*), however, the plumules almost lack a shaft, the latter structure being so rudimentary that it is actually wider than long. In the Tetraonidae and some other galliform birds, where the aftershaft of the contour feathers has its shaft very highly developed with two distinct vanes, the plumules have the shaft likewise developed. In *Lophortyx*, for instance, both shafts of the plumules reach a length of six or seven millimeters, in spite of the small size of the feathers. As pointed out by me (1914), the shaft and aftershaft of plumules,

when both present, are nearly equivalent in size and are practically indistinguishable from each other either by structure or position.

The rami of plumules are extremely long, slender, filamentous, and very numerous, the cellular structure not apparent, and with no edges or dorsal or ventral ridges. The barbules are always of downy type, and have the same structure as the downy barbules of the contour feathers, being of the type found on the aftershaft when this differs from the downy portion of the feather plate, as in gallinaceous birds. As a rule the downy barbules of the plumules are longer and more numerous than those of the contour feathers of the same species, but the difference is often inappreciable. In some genera, e. g., in *Circus*, the barbules of the plumule are more slender than those of the down of contour feathers, and more flexible. The result of the close setting and great length of both rami and barbules, and of their slender, flexible nature, characteristic of most plumules, is a very dense, cottony structure which eminently serves its purpose as a water-proof, heat-insulating covering for the body, as pointed out by me (1914). It is significant that plumules, almost without exception, reach a high development and have a uniform distribution in all water birds.

2. Powder-down

Occurring as a frequent modification of plumules is the so-called "powder-down", a description of which was given by me (1914) in the case of *Circus hudsonius*. Powder-down, according to Gadow (1891), occurs in the following birds: All Ardeae, *Balaeniceps*, *Rhinochetus*, *Eurypyga*, *Mesites*, Tinamidae, a few Falconiformes, some Psittaci, *Podargus*, *Leptosoma*, *Coracias*, and only one passerine genus, *Artamus*. I have also found it in the burrowing owl, *Speotyto cunicularia*.

Although sometimes found scattered promiscuously among the plumules, as in *Gypaëtus* and many parrots, powder-down is usually found in more or less well-defined patches. As Gadow (1891) suggests, the occurrence of powder-down in such diverse groups of birds, and the wide variety of situations in which it is found on individuals, make it appear that typical plumules, at different times and in different groups, may be modified into powder-down, as the result of some unknown stimulation.

3. Oil-gland Feathers

In the majority of birds the oil-gland, occurring on the rump, is furnished with a circlet of feathers at or near its apex, while in others the sides of the glandular swelling are furnished with small feathers and the apical circlet is missing. The presence or absence of this circlet has been used extensively as a taxonomic character. When present the feathers constituting the circlet are of modified plumule type. In *Circus hudsonius*, for instance, the shaft is entirely missing, the calamus splitting immediately into several divisions, which further split into barbs (see Chandler, 1914). There is evidence, in *Circus* at least, that the feathers in the circlet are definite in number.

4. Nestling Feathers

Although no thorough systematic study of the microscopic structure of nestling feathers has been attempted, a brief survey of a few diverse types brings out some interesting facts. The highest development of nestling feathers is displayed in ostriches, in which there is a well-formed calamus. The distal portion of a number of the barbs is more or less expanded and flattened (pl. 13, fig. 2*d*), giving the plumage of the chick a very coarse, bristly appearance. The barbules are numerous, and similar in structure to those of the teleoptiles, only very much shorter. In rheas, as in ostriches, barbules are borne only on the basal portion of the barbs, the tips being hairlike.

In carinate birds the structure of the down barbules of nestling feathers is nearly always less specialized than that of the down of adults. In penguins the minute structure of the neossoptiles or nestling feathers is exactly similar to that of the down of the teleoptiles (pl. 34, fig. 96), the barbules being filamentous with short, sharp prongs at the nodes (see Studer, 1878). In ducks, e. g., *Anas platyrhynchos*, the nestling down differs widely from that of the adults (pl. 35, fig. 104), being exactly similar in form to the down of penguins. The barbules are short and filamentous, with a series of prongs at the nodes, those nearer the tip of the barbules being more prominent than those near the base (compare pl. 35, fig. 104, with pl. 34, fig. 96). The yellow color so characteristic of ducklings is due entirely to structural interference of light. In rails, although the adult down is widely different from that of either ducks or penguins, the nestling down is very similar to that of both these birds, the char-

acteristic black color being due to a uniform distribution of pigment, even in the prongs, thus differing markedly from the adults. The nestling down of *Phalacrocorax* is hardly distinguishable from that described for the other water birds, some of the feathers being black, due to an even distribution of pigment in the barbs and barbules, a few remaining white. In gallinaceous birds, e. g., *Dendragapus*, the nestling down is not quite so primitive, the barbules being longer, with slightly swollen nodes and very inconspicuous prongs, but with evenly distributed pigment.

From an examination of these few types, it may be safely concluded that neossoptiles show a much narrower range of modification in the minute structure of their down than do the teleoptiles, whether plumules or contour feathers. The fact that the structure of adult down in penguins is similar to the nestling down of not only penguins, but also of ducks, rails, and cormorants, may be an argument in favor of the primitive nature of the former birds.

II. FILOPLUMES

1. Occurrence and Distribution

Filoplumes are in some ways the most remarkable modifications of feathers found on birds. Although with a very few exceptions they are excessively slender and very difficult to see with the naked eye, and never developed in sufficient number to be of any possible mechanical use as a covering or support, these inconspicuous feathers are remarkably constant, in some degree of development, in all birds except the ratites. Nitzsch (1867) states that they are probably present in all birds, as he has never looked for them in vain, when the necessary trouble has been taken to find them. This statement, though generally accepted by ornithologists, needs further corroboration. I have been unable to find them in the dried skins of a number of birds, though they may have been present, but so reduced as to be very difficult to discern amongst the other feathers. Such an apparent lack of filoplumes occurred in two species of *Pelecanus* (*P. erythrorhynchus* and *P. californicus*), in *Aechmophorus occidentalis*, and other species. It may be stated positively that they are *not* present in ostriches or cassowaries, and probably not in any of the ratite birds. Nitzsch (1867) described filoplumes from cassowaries, stating that they were coarse, much flattened structures, very different from the filoplumes of other birds, and this has been widely quoted by other authors. Thorough examination of ostriches, both

young and adult, as well as of the back and breast of a cassowary, failed to show any filoplumes whatever. What Nitzsch very probably mistook for filoplumes are the tips of feathers just growing out, which give exactly the appearance described by him for filoplumes.

When present these anomalous feathers are always associated with contour feathers, though not always accompanying *all* feathers of this type; in *Circus hudsonius*, for instance, they could be found only in the dorsal, lumbar, and caudal tracts. When present they grow out in groups from the dorsal side of the socket of the contour feather with which they are associated. There may be only one or two of these in a group, or as many as ten in some water birds, according to Nitzsch (1867). In *Circus hudsonius* there are from five to eight in a bundle, no two in a bundle usually being of the same length.

2. Structure .

As shown by Pycraft (1909), filoplumes are really degenerate feathers, only the barbs of the extreme tip of the feather becoming attached to the slender shaft. The other barbs are formed more or less perfectly, but through a defect in development never become attached to the shaft. Nitzsch reports a case in which some downy barbs and barbules were found near the base of the filoplumes in a specimen of "*Gallus bankiva domestica*." It is very probable that this was an abnormal case in which the development was not arrested as usual, or it may have been a filoplume which had not completed its development, and had not yet lost its deciduous barbs.

Unlike either plumules or contour feathers, filoplumes never have the quill divided into calamus and shaft, the base not becoming hollow and pithy, and the superior umbilicus being absent. The only differentiation at the base of a filoplume is a slight widening and flattening (see Chandler, 1914, pl. 16 fig. 2).

As a rule, full-grown filoplumes have exceedingly slender shafts, often ridged and pitted to give a silvery appearance like a fiber of silk, and they are naked except at the extreme tip, where a few rudimentary barbules are borne directly on the shaft, or on two or three rami which may be given off. In some species they are pigmented, e. g., in the robin, *Planesticus migratorius*, while in closely allied species, e. g., the bluebird, *Sialia mexicana occidentalis*, they have the typical, unpigmented, silvery color.

Although usually entirely covered by the contour feathers, filoplumes are occasionally developed to an extraordinary degree. In many passerine birds they may be seen with a hand-lens projecting beyond the tips of the contour feathers on the nape, while in other closely allied species they may not be exposed at all. In *Planesticus migratorius* and *Sialia mexicana occidentalis*, for example, they are plainly visible in the unruffled plumage, while in *Hylocichla guttata* they are not exposed at all. In many genera of Pycnonotidae they are long and hairlike, giving a conspicuously hairy appearance to the plumage in the region of the nape and upper back.

The only place in which I have found filoplumes really conspicuous is in the plumage of cormorants, more or less in all of the species examined, especially on the neck and upper back, although to some extent on the breast, belly, and rump as well. In these birds many of the filoplumes are long and largely exposed, and have the vanes developed to a very unusual extent. In males they are pure white and show up conspicuously as white streaks against the deep greenish-black color of the contour feathers, while in females they are buffy brown and inconspicuous against the brown plumage. Although their development is very variable, some of them have barbs borne on the terminal four-fifths of the shaft, though there are only about 15 per centimeter on each side, i. e., they are 0.6 mm. or more apart. They are set at a very sharp angle with the shaft, so that they make narrow but fairly dense vanes. The barbs bear very numerous barbules, about 35 per millimeter on each side. They are of a filamentous downy type, but only 0.02 mm. long, and not spread apart to form broad vanules. Although the barbules of the plumules of these species are filamentous, with practically no indication of nodes except at the extreme tip, the nodes on the barbules of the filoplumes are characterized by well-developed sharp prongs, thus resembling the nestling feathers. Though far from what would be expected, filoplumes are by no means conspicuously developed in allied families of Steganopodes; in fact, I have searched in vain for them in dried skins of *Pelecanus erythrorhynchus* and *P. californicus*, *Plotus aninga* and *Phaëthon longicauda*. Since filoplumes occur in the most diverse group of birds, and yet attain such a variable degree of development in birds within the same order, it is a natural presumption that they are of some use in the economy of nature, and are not

merely vestigial or rudimentary structures. No suggestion of a possible use has yet been made.

III. CONTOUR FEATHERS

Under contour feathers, in their various forms and modifications, may be included practically all of the diverse kinds of plumage ordinarily displayed on the body of a bird. In this category come all remiges, rectrices, coverts, and exposed body-feathers, except in a few instances where filoplumes or plumules are exposed, as in cormorants and on the neck of *Pelecanus* respectively; also ear-coverts, eyelashes, rictal and other bristles, and all sorts of ornamental crests and plumes, and other modified feather structures, such as the brush of a turkey, the "wires" of some birds of paradise, the lyre of *Menura*, etc. Their variety of form is almost limitless, yet they are all modifications of the same fundamental structure. A discussion of the various important types of feathers in a typical bird of flight has been made for *Circus hudsonius* by me, (1914) and it is only necessary here to generalize on the conditions found there, and show along what lines phylogenetic modifications of this type have taken place in the whole series of birds.

1. Remiges

a) *Shaft*.—The most highly specialized feathers, those in which the structure reaches its height of perfection, are the remiges, especially the primaries, of strong-flying birds. These feathers, in all flying birds, have a well-developed quill, differentiated into a hollow calamus and a stiff shaft which is more or less rectangular in cross-section, and usually has a groove running along the ventral side, generally quite pronounced at the superior umbilicus and becoming obliterated towards the tip of the feather. The condition of the groove varies to a considerable extent in different groups of birds, in some being broad and shallow, in some narrow and deep, and with all gradations between in others. In the remiges of ostriches the ventral groove of the shaft reaches its maximum size, the shaft in this case being in the form of a half-cylinder, convex above and concave below, while in some of the higher birds, e. g., *Coccyzus*, there is no groove whatever. These facts at first glance would indicate that a large, wide-open ventral groove is a primitive character, that the absence

of a groove is a specialized condition, and that the condition of the groove in the shaft could be used to some extent as a gauge of specialization. This, however, does not hold, since a wide variation can be found, not only within a single group, but in the different feathers of a single species. In less specialized wing quills of a female ostrich, for instance, the shaft has a totally different appearance from that found in the plumes of the male; in the former the shaft is convex above and below, with only a narrow, insignificant groove. In *Coccyzus*, as mentioned above, there is no ventral groove, while in *Geococcyx*, of the same family, there is a broad, shallow groove. In the penguins there is not only no groove, but a median keel is developed both above and below on the very broad, flat shaft. In cassowaries, where the remex quills are reduced to bare, stout spines, there is no groove, and the shaft is subcircular in cross-section. Aftershafts are never developed on remiges.

b) *Vanes and Barbs*.—The vanes of remiges of flight birds are never quite equal, the outer vane always being narrower than the inner, very conspicuously so on the outer primaries, often subequal on the inner secondaries. In many of the best birds of flight, especially those which soar and glide to a considerable extent, there is a further modification of the vanes of some of the outer primaries, in that more or less of the distal portion is narrowed down or "incised" so that the tips of these feathers, when the wing is spread, are separated from one another like spread fingers. In the columbid genus *Drepanoptila*, the feather plate is bifurcated, there being distally two shafts and four vanes. This anomalous condition, characteristic of the trunk feathers of other genera of the same group of Columbidae, must be regarded as a recent, heritable mutation.

Usually more or less of the basal portion of the vanes of remiges, as well as of other contour feathers, is downy in character, though often the innermost portion of even the most basal barbs may have pennaceous or transitional barbules, a larger and larger portion becoming downy as the superior umbilicus is approached (fig. A). In flightless birds various kinds of reduction of the vanes of remiges takes place. In ostriches the remiges are developed in the male as ornamental plumes, in cassowaries they are reduced to stiff, bare spines, with the vanes absent entirely, while in penguins and most other flightless birds they are reduced to the condition of the trunk feathers, and are barely, if at all, distinguishable from them.

Although the narrowness of the outer vane in the primaries is brought about partially by an actual shortness of the barb, it is accentuated by the relatively narrower angle which the barbs of the outer vane make with the shaft. In all but the most generalized remiges, there is a tendency for the barbs of the outer vane to be inserted farther apart on the shaft, but at a more acute angle than those of the inner vane. As a rule, the number of barbs per unit of measure changes in a very definite manner, following a mathematical curve analogous to some of those worked out by Pearl (1907) for growth in the whorls of leaves of the aquatic plant *Ceratophyllum*. Beginning at the tip there is a slight decrease in number per unit of measure, then a very slowly accelerating increase for the greater length of the feather, terminating in a very quickly accelerating increase as the superior umbilicus is approached, accompanied by a transition to a downy form. It is interesting to note in this connection that *the change in number of barbules per unit of measure on the barbs follows a very similar curve*, and probably varies with a similar mathematical equation.

The barbs of remiges, with the exception of the meager basal downy structure already mentioned, are always highly developed in birds of flight, consisting of a thin lamelliform ramus bearing highly developed distal and proximal vanules (Fig. B). The pith of the ramus, as shown by Mascha (1904), is composed either of a single dorso-ventral plate of cells, one cell in thickness, or of a network of cells, more than one cell in thickness (Fig. C).

Without exception, the rami of the inner vane are narrower than those of the outer, though often almost imperceptibly so. Distal to the notch of the incised primaries this difference is especially noticeable, the rami of the outer vane being often as deep as the shaft, while those of the inner vane are less than half as deep. In the majority of birds where the rami are not as deep as the shaft, there are fine ridges on the shaft from the insertion of the ramus to the ventral edge. As pointed out by me (1914), the deep type of ramus is probably the more primitive condition.

The ventral edges of the rami (fig. C) are produced into horny keels, usually with no evident cell structure, known as the ventral ridges (see Pycraft, 1893; Mascha, 1904; and Stubbs, 1910). Although in the great majority of birds this ridge forms only a narrow, inconspicuous border for the ramus, in a few birds it is extra-

ordinarily developed as a very thin, translucent film, which bends distally and overlaps the following ramus, giving a smooth, glazed appearance to the under surface of the feather which is conspicuous at the most casual glance. It is thus developed in all of the Anseres, (pl. 33, fig. 28a), and in a number of gallinaceous birds, though in the latter it is by no means constant, being present, for instance, in *Bonasa*, but absent in *Lophortyx*. The ventral ridge of the outer vanes of some groups of birds, e. g., Anseres, Falconidae, and some Ciconiae, is further modified by being furnished with irregular villi (fig. C, and pl. 21, fig. 28b) on the ventral edge. The rami of the inner vane always have the ventral edge entire or nearly so.

As shown by Mascha (1904), rami are furnished with a lateral "ledge" which is grooved for the reception of the bases of the barbules (fig. C). These are much more highly developed and efficient in some birds than in others, often making it very difficult to scrape off the barbules without tearing off with them a part of the barb to which they remain attached.

c) *Barbules*.—The interlocking barbules of a typical remex are of four distinct types, the distal and proximal barbules of the inner vane, and the distal and proximal barbules of the outer vane.

It is unnecessary here to enter into a discussion of the typical structure of distal and proximal barbules, or of their manner of interlocking. An excellent description of this is given by Pycraft (1893), and a few additional facts of interest are added by Mascha (1904). There are, however, a number of minor details of structure of both distal and proximal barbules which are almost uniformly different in all birds in the inner and outer vane, although apparently this fact has escaped the notice of all previous observers. As a rule the bases of the distal barbules of the outer vane are longer and relatively narrower than those of distal barbules of inner vanes, but this is not always true, the chief difference lying in the pennula. On the inner vane the pennulum of distal barbules as a rule is longer than it is in the outer vane, with fewer hooklets, but a larger number of cells with cilia (compare pl. 16, fig. 8a, with fig. 8c and see text-figure D). The most conspicuous difference lies in the dorsal cilia on the proximal portion of the pennulum. Almost without exception, distal barbules of the inner vanes of remiges are characterized by the specialized development of the first two (pl. 20, fig. 20a), and often to a less extent of the third, dorsal cilia (pl. 20, fig. 23a). These specialized cilia are developed as stout, conspicuous, lobate, or

thornlike projections, which are directed more or less distad, i. e., toward the tip of the feather (see plates). In the Falconidae they differ from the other dorsal cilia only in being slightly stouter and more thornlike (pl. 23, figs. 36a, 37a, 38a, 39a, 40a); in owls they are well developed but not differentiated from the other cilia (pl. 32, fig. 84a); while in a few birds, e. g. trogons (pl. 31, fig. 80a), they are absent entirely. On the outer vane, on the other hand, the dorsal cilia of the proximal portion of the pennulum are always absent, at least on the first two or three cells; very frequently no dorsal cilia whatever are present. Usually, however, following the proximal two or three cells, rudimentary barbicels begin to appear, and these become more and more pronounced distad, the reverse condition to that found on the inner vane. With the exception of these few details, the structure of distal barbules of both inner and outer vanes is usually alike, and both show the same group characteristics.

The proximal barbules (fig. E) of the two vanes are nearly always exactly similar in more or less of the basal portion of the barbs, but in the majority of birds they differ in the more distal portion of the barb, sometimes only at the tip, more frequently in from one-third to two-thirds of the terminal portion. Those of the inner vane, and those which are similar to them on the outer vane, have rather long slender bases, considerably longer than the bases of the distals, a series of three to six ventral teeth of differing degrees of development in different birds, and more or less filamentous pennula with only very rudimentary barbicels if any at all. With a few exceptions, notably most of the ciconiiform birds, the more distal proximals of the outer vane differ decidedly from the others in the development of a series of ventral barbicels, these being formed as an increased number of ventral teeth, accompanied by a change in form. In many birds these ventral barbicels, homologous to the hooklets and ventral cilia of distal barbules, are very large and numerous and highly conspicuous, e. g., in gallinaceous and falconid birds (pl. 23, fig. 38c, and pl. 24, fig. 42e). Perhaps the greatest development is that found in *Ceryle alcyon* (pl. 31, fig. 79a). In many passerine birds, e. g., in all the Tyrranidae, the outer half of the barbs undergoes a very sudden and conspicuous change from plain to barbicelled proximal barbules (compare plate 33, fig. 92d with plate 33, fig. 93a), this sudden transition including a very marked reduction in the size of the base, and a concomitant simplification of the distal barbules, the hooklets of which become obsolete. This change in structure

produces the fringe, or edge, usually of a paler color, so frequently found on the remiges and coverts of passerine birds.

Usually the structure of barbules, except for variations already mentioned, varies but little on different portions of the same barb or of the same feather. At the base of the barb there is a decided shortening of both kinds of barbules, while at the tip the change is in the nature of a loss of the perfection of structure. Usually, also, the distal barbules of the inner vane have the specialized dorsal cilia better developed on the terminal than on the basal portion of the barb.

Surveying the entire class of birds, we find that the pennaceous barbules vary considerably in the different orders and suborders, though usually being fairly constant within the lesser groups, except where modified for color production, or other conspicuous effect. Differences occur in size and shape of the bases, position of nuclei, form of pennulum, and nature of all the different types of barbicels. In tinamous alone a most remarkable modification of the typical vanules occurs in the solid secondary fusion of the pennula of the proximal barbules, except at the extreme tip of the barbule, to form a limiting bar parallel to the barb (pl. 25, figs. 49*b* and *e*). Though this surprising modification is absolutely characteristic of all tinamous, not only of the remiges, but of all the other pennaceous contour feathers, I have found no suggestion of it in any other birds, and I have been unable to find any reference to it in the literature.

2. *Rectrices*

With this brief survey of the conditions found in the remiges of birds, we may now turn to the other groups of contour feathers. Next to the remiges, the most highly developed feathers of the body, in birds of strong and graceful flight, are the rectrices. The macroscopic form of the tail and of its individual feathers varies considerably, and the microscopic structure is far more subject to modifications for special functions than it is in the remiges. In normal rectrices, used in flight for steering and balancing, the structure is very similar to that of the inner remiges, and it is interesting to note that in the *middle* tail feathers *both* vanes have a type of structure of barbules similar to that characteristic of the outer vane of remiges. In ratite birds there are no specialized rectrices among the Casuariiformes or the Apterygiiformes, while in the Struthioniformes and the Rheiformes the rectrices are large and developed as

ornamental plumes. In penguins and Colymbiformes they are indistinct. In a few birds, e. g., *Menura*, they are transformed into an ornament, although it is more frequently the upper tail coverts that are modified to produce an ornamental tail. In woodpeckers, swifts, and a number of other birds the rectrices have the plate undeveloped at the tip, and the bare shafts enlarged as stout spines to aid in climbing or bracing against a steep surface. Like the remiges, the rectrices never possess aftershafts.

3. *Unspecialized Contour Feathers*

Passing now to the *coverts*, we find that in them there is a complete transition from the remex type of structure to that found in the contour feathers of the trunk, the greater coverts being more like the former, some of the lesser ones very much like the latter. We may pass at once, therefore, to a discussion of the morphology of the trunk feathers.

a) *Aftershafts*.—These feathers in the majority of birds are characterized by the presence of an aftershaft, and the presence or absence of this structure has been considered of considerable taxonomic importance. The condition of the aftershaft in the various groups of birds is given in the table on page 256.

A great deal of variation exists, as will be seen, within single suborders or even families. Within the Ratitae there is an extreme variation from a total absence in the ostriches, rheas and *Apteryx*, to a maximum size, practically equivalent to the main shaft, in cassowaries and emus. Various types of aftershafts occur in carinate birds, the most common form being one with a very short shaft and long, spreading barbs, very similar in form to plumules. In many gallinaceous birds, e. g., in the Tetraonidae, the aftershaft reaches a very high degree of development, its shaft being frequently three-fourths of the length of the main shaft, with its vanes coherent and of even width throughout (fig. A). The usual type in passerine birds, on the other hand, is very different; the shaft is extremely short, with a few short rudimentary barbs near the base, followed by four to eight very long, free barbs, entirely disconnected from each other. The barbs and barbules of aftershafts are always of downy structure, the minute characteristics of the barbules being usually the same as those of the down of the main feather plate, but there are a number of exceptions to this, e. g., in the gallinaceous and passerine birds. In such cases the structure is less specialized

than that of the down of the feather proper, and differs in not possessing certain specialized characteristics, such as the detachable rings at the nodes found in the more basal barbules of gallinaceous birds (pl. 36, fig. 108), and the fimbriae which characterize the base of the inner barbules in passerine birds (pl. 37, figs. 114 and 115).

b) Down.—In all but especially modified contour feathers, a varying proportion of the feather plate is downy, the transition from the downy to the pennaceous portion being sometimes gradual, but more frequently abrupt, as shown in text—figure A, the line of demarcation varying a great deal in different feathers. In the lower belly feathers and tail coverts of some birds, e. g., *Leptoptilus*, the downy structure pervades the entire feather, producing the “sempiplies” of Nitzsch (1867) and others. In *Leptoptilus* these are the feathers from which the true “marabou” of commerce is derived. Feathers very similar to these are developed in the lower belly region of turkeys, these being employed very extensively as a substitute for “marabou”.

The minute structure of the down varies to a large extent in different groups of birds, the nodes and internodes both displaying peculiarities which are highly characteristic of different groups (pls. 34-37).

The structure of down often varies a great deal in a single feather, the specific characteristics being always best displayed by barbules on the inner portion of the distal vanule of the basal barbs. Farther distad on either feather or barb, and on the proximal vanules, the structure is often less specialized, and lacks some of the characteristic features of the group. This is well displayed in the down of a turkey, where only the inner portion of the distal vanules of barbs on the basal part of the plate possess the peculiar, characteristic, detachable rings at the nodes (pl. 36, fig. 108). The structure of the proximal vanules of the same region of the feather often approximates that of the distal vanules, but is never quite so perfect. The outer barbules of all the barbs, and all the barbules of the more distal barbs, lose the specialization, becoming finally filamentous with the nodes very inconspicuous. Though this is the order of reduction of specialization where such reduction takes place, there are some birds in which the downy structure, though highly specialized, is almost uniform, becoming reduced only at the tips of the barbs, as in the Anatidae. As stated above, the structure of the down of aftershafts and plumules, but not of neossophtes, is

similar to that of the *proximal* vanules of the downy barbs of the feather proper, in case there is any special modification in the distal vanules, as in gallinaceous birds.

c) *Pennaceous Barbules*.—Concerning the pennaceous portion of contour feathers of the trunk, all degrees of development of structure can be found. In ratite birds, as is well known, there is never any pennaceous structure developed, although the bases of the barbules in *Rhea* (pl. 13, fig. 1a) are exceptionally well developed for down, and seem to indicate a transition to or from a pennaceous type of barbule. In typical trunk feathers there is no differentiation of inner and outer vanes, and usually the structure is a mere simplification of that found in the more highly specialized remiges. In the contour feathers of the trunk, as would be expected, the distal barbules are of the type of the outer vane of the remiges, and the proximal barbules of the type of the inner vane of the remiges, often in very degenerate form, these types being the ones showing the lesser degree of specialization. In the trunk feathers the conspicuous basal dorsal cilia are seldom developed on distal barbules, and ventral cilia seldom occur on the proximal barbules (pl. 20, figs. 20e and f). In a great many birds these structures in trunk feathers are very much simpler than they are in the remiges, all of the barbicels being very much reduced or even absent. In distal barbules the cilia often disappear entirely, the hooklets are reduced to one or two very weak ones, and the ventral teeth are represented only by a very small, inconspicuous projection (pl. 33, fig. 92e); the proximal barbules frequently lose the sharp differentiation between base and pennulum, becoming evenly tapering all the way to the tip (pl. 33, fig. 92f). Such modifications are always farther advanced on the breast and belly feathers than on those of the back, the back feathers often being intermediate between the remiges and coverts on the one hand, and the breast and belly feathers on the other.

In some birds the pennaceous barbules of trunk feathers have special modifications of their own, and, as might be expected, these are usually more conspicuous and better developed on breast than on back feathers. The most peculiar structural modification characteristic of trunk feathers only, and the only one which needs special mention here, is the development of curved dorsal barbicels on the base of both distal and proximal barbules (pl. 17, fig. 10e, 12a, b). Since these barbicels are not homologous with any other types of

barbicels, and are always of the same curved form, they have been given a special name, *flexules*.

Though totally absent in the majority of birds they are very characteristic of several groups, namely, Procellariiformes, Gruiformes, and Laro-limicolae (pls. 17, 26 and 28). They are usually not present on some of the basal barbules, but are generally characteristic of a considerable portion of the distal vanule, and usually a little less of the proximal vanule. In distal barbules they first develop at the proximal end of the base (pl. 16, fig. 8e) and progress toward the pennulum, ultimately forming a continuous series with a similar series of pennular dorsal barbicels. This, however, does not happen until the hooklets are lost, since hooklet cells never possess dorsal barbicels of any sort. The result of this is often a conspicuous break in the dorsal series of barbicels on the barbules which still retain the hooklets (pl. 26, figs. 52d, e, and f). In proximal barbules the flexules develop first at the distal end of the base as a direct continuation of the pennular series (pl. 16, fig. 52g, h).

4. Ornamental Plumes

Frequently some of the contour feathers of the trunk are especially modified as ornamental plumes, the variety of form displayed by them being very great. There is hardly any group of contour feathers which may not at one time or another, in different groups, become modified as ornamental plumes. Among such feathers may be mentioned the diverse kinds of crests developed in many birds, the "aigrettes" of various species of herons, the ruffs and tail plumes of pheasants, the gorgeous upper tail coverts of peacocks and trogons, and the very great number of feather modifications in the various species of birds of paradise. Nearly all of these modified plumes are produced either by a mere elongation of the feathers concerned, by an even decomposition of the vanes, or, as in the crest of *Goura* and the upper tail coverts of peacocks, by an uneven decomposition, resulting in the production of ocelli, rackets, etc.

Although in such decomposed vanes as are found in the "aigrettes" of herons, in the crest feathers of *Goura*, or in the commercial "paradise-plumes" (chiefly the under wing coverts of *Paradisaea apoda*), the barbs are widely separated from each other on the shaft, and appear macroscopically to be devoid of barbules, closer examination shows that a more or less complete series of degenerate barbules are present, closely appressed to the shaft. In very few

cases are the barbules lost, except in connection with color production, or in case of the tips of the barbs being transformed into stiff spines as in the tails of woodpeckers. A farther modification found in contour feathers is the formation of a terminal undivided horny expansion, produced either by the shaft alone, as in certain rail feathers (Bonhote, 1912), by the coalescence of the shaft and both vanes, as in the crown feathers of the curly-headed toucan (*Pteroglossus beauharnaisi*), or by the fusion of the shaft with the terminal portion of only the outer vane, as in the "wax tips" of *Bombycilla garrula* (pl. 33, fig. 95a).

5. Ear Coverts

On the head of most birds there are a number of modifications of contour feathers to serve special functions, and they are wonderfully adapted to serve their particular purpose.

First among these may be mentioned the ear coverts. The typical structure of these feathers is similar to that described by me (1914) in *Circus hudsonius*. They are loose-vaned feathers, with the barbs wide apart on the shaft, and the short, awl-shaped, degenerate pennaceous barbules closely appressed to the barbs, thus producing a mechanism admirably fitted to catch dust particles and yet not obstruct sound. In birds which have well-developed after-shafts this structure is also present in the ear coverts, but in much modified form. In the Limicolae, herons, hawks, and some others, the aftershaft is greatly developed and almost equals the main feather in both size and structure. In Tetraonidae the aftershaft is reduced to a very small downy pad, scarcely larger than a pin-head, which takes no part in covering the ear. An intermediate condition occurs in *Grus*, where the basal portion of the aftershaft is densely downy, while a few of the barbs are elongated, with the typical appressed, inconspicuous barbules. In owls and many other coraciiform and many passerine birds, the ear coverts lack an after-shaft entirely. As has previously been pointed out (Chandler, 1914), the ear coverts are undoubtedly adaptive modifications of contour feathers, which are in a transitional stage of transformation ultimately leading to the various kinds of facial bristles and eyelashes.

6. Facial Bristles and Eyelashes

The steps in transformation from ordinary contour feathers of the trunk to the highly modified eyelashes of certain birds may

be traced without a break in such a bird as *Circus hudsonius*, as has been done by me (1914). As was shown there, after the diminution in number of barbs and reduction of barbules, as is the condition in ear coverts, the next step is the complete loss of the terminal barbs and elongation of the shaft into a bristle. Then follows the loss of more and more barbs and stiffening of the shaft, until the latter becomes a stout, unbranched bristle, as in the eyelashes of many birds. Usually rictal, supraorbital, and nasal bristles have some of the barbs still present; in the dense nasal tuft of *Corvus* the structure is very much like that of ear coverts, except that the barbs are set at a more acute angle with the shaft, thus producing narrower vanes. Comparatively few birds possess eyelashes, but when present they are so modified that in some cases nothing remains but the stout, deeply pigmented quill, totally devoid of any barbs or barbules. Such is the case in hornbills, *Geococcyx*, and some other birds. In birds with aftershafts, although the main shaft is entirely bare, the former is represented by a few small, weak barbs with rudimentary barbules, e. g., *Circus*, *Cathartes*, and some others.

7. Facial Ruffs

In a few birds, e. g., owls and *Circus*, facial ruffs are developed, composed of several rows of closely grouped, very compact, curved feathers. The shafts are stiff and inserted almost at right angles to the surface of the body, only the tips being curved so as to lie flat on the contour. The solid compact vanes are made so by the close approximation of the barbs to each other, and by the exceedingly numerous barbules which have well-formed and characteristic barbicels, but are short, due to the shortness of the individual cells, an obvious correlation with the close approximation of the barbs.

IV. COLOR PRODUCTION

1. *Isotely in Production of Colors*

The colors of feathers have been studied by a great many workers, chief among whom may be mentioned Altum (1854a, 1854b), Bogdanow (1856), Fatio (1886), Church (1893), Krukenberg (1882), Gadow (1882), and Strong (1902). As shown by the researches of these men and others, the colors of feathers fall into three cate-

gories, namely, pigment colors, structural colors, and compounded colors, produced by combinations of pigment and structure in different parts of the same barb.

It is not the purpose of the present chapter to deal with pigments or methods of actual color production, except in so far as the morphology of the feather parts is concerned, but to show what different modifications occur in feathers of different groups of birds to produce the same results, i. e., *isotely*, to use a word coined by Gadow (1911) to mean the attainment of a similar end by different processes in different organisms.

Colors which are produced by a single pigment, evenly distributed in the rami and barbules, with no objective color effects, seldom involve any modification in the morphology of the barbs. For example, in feathers which have light and dark bars in which the colors are of purely pigment origin, there is no appreciable difference in the form of the barbs in the light and dark areas. The only colors which are produced merely by an even distribution of pigment are blacks, browns, including rufous, and lemon yellow. Although red occurs very frequently as a pigment, it is almost always accompanied by some structural modification. In the Musophagidae there occurs a green pigment, turacoverdin, which is not accompanied by any special structural modification. Grays, tinged with bluish, ranging from pale pearl gray to deep slate gray, are usually produced by an uneven distribution of black or dark brown pigment. In gulls and columbid birds, for instance, the characteristic gray colors are produced by conspicuous transverse bars of dark pigment on a transparent background in the barbules (pl. 29, figs. 70c, d). In herons nearly the same effect is obtained by a dilute, even pigmentation in the bases of the barbules, supplemented by elongated unpigmented pennula (pl. 20, fig. 20e). The same method is employed to produce the hoary color of terns and other birds, except that in this case the effect of the unpigmented pennula is accentuated by the long, brush-like ventral cilia. A pretty olive-green color is produced in the back feathers of *Osmotreron vernans* by a combination of slate and lemon yellow, the former being the effect of dark pigment bars in the transparent bases of the barbules, the latter produced by a lemon-yellow pigment in the pennula, which have large blunt ventral cilia (pl. 29, fig. 69a).

Structural colors, i. e., colors which are produced by modifications of structures causing interference or diffraction of light, may

be produced by the rami alone, or by the barbules alone. Although the physical principles upon which the color production rests are probably very much the same in all cases, the mechanisms or surfaces for producing it vary to an astonishing extent in different kinds of birds; the same color is by no means always produced in the same way.

As a rule, white is produced merely by the absence of pigment, the barbules being translucent, or semi-transparent, and producing a white color by the diffusion of light by means of the numerous edges and irregularities of surface of the vanules. In some cases, however, more complicated mechanisms are resorted to. In *Lagopus* the barbules from a white feather appear a peculiar fawn-gray color under the microscope by transmitted light, due to the presence of an infinite number of exceedingly small air bubbles in the substance of the barbules (pl. 24, fig. 47a). When the latter are broken, (i. e., the horny outer sheath rendered penetrable) and immersed in balsam, the latter substance, which has almost exactly the same refractive index as the substance of the feather, destroys the effect of these bubbles by filling in the air spaces, and it is rendered transparent. In many feathers which have conspicuously white shafts or barbs, all or a portion of the barb is filled with a mass of these minute bubbles, appearing under the microscope dark and opaque by transmitted light, but glistening white, like a miniature snow bank, by reflected light. Such a phenomenon may be seen on the lower side of the rami of belly feathers of *Asyndesmus*.

The silvery straw color found on the outer vanes of the secondaries, wing coverts, and scapulars of *Plotus ankinga* is produced in an absolutely unique way. The proximal barbules and bases of the distal barbules are black, while the tips of the distals are highly modified, inflated, and without pigment, though scattering the light in the same manner as the rami of *Asyndesmus* (pl. 18, figs. 13c, e). Like the white rami of the latter, they are rendered transparent when pervaded by balsam.

Yellow is sometimes produced by pigment alone, especially in such yellows as those of orioles and wood-warblers, and is then usually produced by pigment in both rami and barbules. Many yellow feathers, e. g., the straw yellow of the head and neck of *Paradisaea apoda*, possess little if any pigment, and have their color produced by naked rami with longitudinal grooves, or irregular pits. When crushed they are rendered transparent and colorless, and show no

color by reflected light. More frequently, as in the belly of *Myiarchus* and *Tyrannus verticalis*, the color is a combination of yellow pigment and the same superstructure as described above.

Orange and red, like yellow, may be produced by pigment alone, by a combination of red pigment and a structural modification, or by a structural modification with an underlying dark pigment. The simplest red is that produced by a diffuse red pigment in both rami and barbules, with no structural modification, as in *Cardinalis cardinalis*. A much deeper and more striking red is produced by a mere glazing or highly polished surface of barbules or naked barbs filled with red pigment, as in the deep red of *Nectarinia famosa*, or the "wax tips" of the waxwing. It is a common phenomenon for red feathers to be characterized by comparatively widely separated transverse ridges of one sort or another on the barbs or barbules. In *Eudocimus ruber*, *Phoenicopterus ruber*, and some other species, the barbules are inflated, possess a rather dilute red pigment, and have the margins of the cells conspicuously enlarged as ridges (pl. 20, fig. 26a). In the fiery red crest of *Tyrannus verticalis* the red pigmented barbs have similar transverse striations, produced by rudimentary scale-like barbules, arrested in their development, and fused with the ramus. In hummingbirds only, so far as I have observed, is red produced by iridescence. In the red gorget feathers of many species of hummingbirds, the color is produced by the greatly developed flange, which is broader than the rest of the base of the barbule. and has no apparent striations (pl. 32, fig. 88d). The underlying color is a very dark olive, quite different from the fuscous brown underlying iridescent green or the rufous brown of iridescent blue, a phenomenon which may be explained by the principle of selective transmission and reflection.

Green is produced in a very large variety of ways. In the Musophagidae alone there is a green pigment, turacoverdin; in *Osmotreron* and a few other birds, some of the feathers appear green from a combination of greenish yellow in the pennula, with some gray or blue color in the bases (pl. 29, fig. 69a). In *Melopsittacus* a delicate blue-green results from a blue refraction color in the rami, coupled with a greenish-yellow pigment in the barbules. In the vast majority of cases green is an iridescent color, and is the commonest iridescent color found in birds. The variety of refrangent surfaces is astonishing. In the speculum feathers of ducks, for instance, the cells of the pennula are highly modified into flat, warped

structures with a very dark pigment (pl. 21, fig. 28*i*); in the green feathers of pheasants and roosters the pennula are modified into spoon-shaped, flat structures with deep pigmentation, with no warping of the individual cells, or constrictions between them (pl. 24, fig. 42*g*); in the peacock, green is produced by barbules which are conspicuously ringed or cross-ridged in both base and pennulum; in hummingbirds by the greatly developed flange of the bases of the barbules (pl. 32, fig. 88*d*); in trogons by smooth, curved barbules (pl. 31, fig. 81*a*), more or less triangular in cross-section, devoid of barbicels of any kind, and entirely given over to the production of color, the effect of tinsel being consequent upon the broken surface, resulting from the irregular curving of the barbules; in *Nectarinia famosa* by short, flattened barbules, with no barbicels whatever, the entire barbule very closely resembling the pennulum of a green duck feather; and in parrots, coraciids, etc., by the rami alone, in which the greatly developed dorsal ridge is refrangent, the tone of the color varying with the amount of black or brown pigment in the non-refractive barbules. Bronze is produced in manners very similar to those of refraction greens.

Blue, except the slate blue of *Goura*, or bluish-gray as of herons and pigeons, is always a refraction color, produced in nearly all the same ways as is green, but always underlaid by a warmer brown pigment in accordance with the principle of selective reflection. The pretty light blue of *Coracias affinis* and some other species is produced by a deep violet refraction color in the hexagonal cells of the ramus, each hexagon, or sometimes only scattered ones, being overlaid by a whitish film which is destroyed by scraping or by crushing which is insufficient to destroy the deeper refraction color. In the case of the light blue, the barbules are transparent.

Various delicate and unusual colors are produced by a combination of structural color in the ramus with a pigment color in the barbules, e. g., in *Melopsittacus*, already cited, and in the blossom-headed parakeet, *Palaeornis cyanocephalus*, in which the delicate changeable color, "resembling the bloom of a peach", is the result of a combination of a blue refraction color in the rami, and a red pigment in the barbules.

It is apparent from this that a great many different methods have been employed in nature in the acquisition of similar results, totally independent of each other, as much so as are the various types of wings produced in insects, reptiles, birds and mammals.

I can think of no more striking example of isotely, the attainment of the same end by different methods in different groups, than these manifold methods of producing a single color.

2. Effect of Albinism on Structural Color Modifications

One of the most remarkable things about the morphology of feathers is the profound change of structure so frequently involved in the production of color effect, in spite of the surprising constancy of group characters where no such color modifications occur. It was with extreme interest that the writer examined some of the feathers of an albino mallard, *Anas platyrhynchos*, to see whether the morphologic modifications involved in the production of the violet speculum would be lost or retained with the lack of pigment. It was found that the distal barbules of the outer vane, which in a normal mallard have the pennula highly modified for the production of color (pl. 21, fig. 28a); lacked this modification entirely, and were exactly similar to the normal distal barbules of the outer vane of feathers of this species in which there was no modification for color (pl. 21, fig. 28e). In other words, *the constitutional factor causing the morphologic specialization of feather structures for the production of color is inseparably bound together with the factor for the accompanying pigment, and if the latter is absent, the feather structures present the normal type of the species in which there are no color modifications.*

PART II

SYSTEMATIC

INTRODUCTION

After making a careful study of the modifications of plumage of a single individual bird of a representative species, namely, *Circus hudsonius* (Chandler, 1914), and after making a general survey of the entire class of birds to find out in how far the phenomena there found are applicable to birds in general, a systematic study was made of each order of birds in succession to find out what, if any, modifications of feather structure were characteristic of, or peculiar to, the order or other group in question, and to determine the extent of variation to be found in the group, and to work out, if possible, the probable phylogenetic relationships on the basis of feather structure.

1. *Intraspecific and Phylogenetic Modifications*

At the outset it was necessary to determine how much individual, seasonal, or sexual modification in structure might exist within a species. Examination of a series of birds, in any group in which this has been attempted, shows conclusively that the corresponding feathers of any individuals of a species normally show no appreciable variation from each other, providing the age, sex, season, and other conditions of the specimens be comparable. In other words, *comparable specimens of a species possess a definite, typical feather structure which is normally invariable, as much so as are the muscles, bones, or any other system of the body.* Abnormalities and wear may produce considerable changes, but they need not be considered at length here. Fault bars in feathers, for instance, resulting from inadequate nutrition or some other unfavorable condition, produce areas of imperfectly formed barbs; albinism, as shown on page 279, makes a feather which normally possesses a modification in structure for the production of color revert to the normal species type; wear and soiling often give the minute structure a very different appearance; and it is possible that other foreign influences may considerably alter the form and structure of feathers, but these all

come under the head of pathogenic conditions, and need no further consideration here.

Age, seasonal, and sexual variations in feathers occur only when needed for the production of a special result. Just as the greater coverts of a bird may differ in microscopic structure from the middle coverts in order to produce a different macroscopic effect, so in some birds certain of the feathers in the spring plumage may differ from the corresponding ones in the fall plumage, in order to bring about a different total effect. Sexual differences in minute feather structure may likewise exist, but only to produce a macroscopic appearance which is a secondary sexual character, e. g., elongated plumes, crests, color effect, etc. Differences in microscopic feather structure are not, in themselves, secondary sexual characters, but are merely employed in the production of more obvious secondary characters. In a few cases variations in feather structure are employed to produce different effects in different ages, even though in the same seasonal dress, as for instance in many of the orioles, whose plumage pattern in the spring of the second year differs from that of the third year. Such changes are rare and occur only in the first few years; when the ultimate adult plumage is attained, no further age variations occur.

As a rule, there are no considerable variations in the feather structure of different species of the same genus, except, as in the case of intraspecific variations, when instrumental in the production of some larger specific difference. Species, of course, are by no means of equal rank, and in subspecies or in slightly differentiated species feather structure, *per se*, cannot be used as a taxonomic character, although very slight differences in similar feathers do sometimes exist in widely different species of a single genus. Moreover, generic differences in feather structure may usually be passed over, since they are ordinarily so slight that they cannot positively be distinguished at all, or only with intensive study, and then *only in case it is certain that the portion examined comes from an exactly similar part of a corresponding feather*.

In all groups higher than genera, however, epiphylogenic differences may almost always be detected. In other words, it is usually possible to distinguish, by details of feather structure, any feather of a specimen of a given family from any approximately similar feather of a specimen of another family, even if in the same sub-order. The amount of differentiation, however, is extremely vari-

able, in some cases being scarcely noticeable, while in others it is very apparent. In the Steganopodes, for instance, the difference in feather morphology in some of the different families is very great, while in the families of Passeriformes, which, as a matter of fact, are hardly more than supergenera, it is extremely difficult to distinguish between even widely separated ones. This difference in degree of differentiation also holds true for groups of higher rank. As intimated above, to be comparable the feathers whose parts are to be compared must be approximately similar, since there is frequently more variation between different kinds of feathers on a single body than between corresponding feathers of birds of different orders. For example, the barbules of a remex of *Larus* differ in their minute structure from those of a breast feather of the same genus far more than they differ from those of a remex of a loon, for instance.

2. Classification Adopted

The problem of what recognized system of classification to follow in the study of comparative feather morphology presents itself at this point. To the mind of the writer the system which represents most clearly the true relationships of birds according to the present status of our knowledge concerning them, and one that is coming into very general favor with ornithologists in this country as well as in Europe, is that presented by Knowlton and Ridgway in the *Birds of the World* (1909). This classification, as stated by Knowlton, is essentially the same as that used by Gadow (1891), modified in some details by the later researches of ornithological workers. Although this classification was adopted in the present study as a mere working basis, it was found that as far as feather morphology was concerned it is apparently a more natural grouping than any other; yet, as will be shown in the following pages, there are some possible changes in it suggested by feather structure, and a hypothetical revision of it, based primarily on the latter, will be suggested at the close of this paper.

In the systematic discussion of the various groups, the grouping and succession used by Knowlton has been used with only two exceptions. The Struthioniformes, Rheiformes, Casuariiformes and Apterygiformes have been included under a common heading *Ratitae*, as has usually been done, while the Crypturiformes have been dissociated from these and placed immediately after the Galliformes,

where, according to their epiphyloggy, they seem to belong. The classification as here used is as follows:

CLASS AVES

Subclass Neornithes

I. Ratitae

Order Struthioniformes

Rheiformes

Casuariiformes

Apterygiformes

II. Carinatae

Order Sphenisciformes

Colymbiformes

Procellariiformes

Ciconiiformes

Suborder Steganopodes

Ardeae

Ciconiae

Phoenicopter

Order Anseriformes

Suborder Anseres

Palamedeae

Order Falconiformes

Suborder Cathartae

Gypogerani

Accipitres

Order Galliformes

Suborder Galli

Turnices

Order Crypturiformes

Gruiformes

Charadriiformes

Suborder Larolimicolae

Pteroclo-columbae

Order Cuculiformes

Coraciiformes

Suborder Coraciae

Striges

Caprimulgi

Cypseli

Coli

Trogones

Pici

Order Passeriformes

3. *Methods of Comparative Study*

In working over the morphology of feathers in each of the above groups, a brief survey of feather structure was made of a series

of representative species, representing both the typical and outlying forms included, and then a species which seemed to be fairly typical for the entire group was selected for careful study, and the minute structure of its remiges and body feathers worked out in detail. So far as possible, except in the Passeriformes, representatives, usually several, of each included family were examined to determine the constancy of the characters found in the selected type, and where important differences were found in other groups of the same order or suborder, their epiphylogeny was also worked out in detail:

Since it was obviously not possible to examine more than a few feathers of each bird studied, similar feathers, as far as possible, were studied in each group taken up, namely, both inner and outer vane of a typical remex (i. e., not a highly specialized outer primary or a weakened inner secondary), a back feather, and a breast feather, though in many cases the latter two were so similar that they did not merit separate descriptions. In other words, the method of study of groups has been: (1) a detailed study of representative feathers of a type, and (2) a study of a number of other selected species, to determine the constancy or modifiability of the characters observed in the type, and to discover the presence or absence of further or different modifications. A discussion of the relationships suggested by feather morphology, and a review and summary of the epiphylogeny is given at the end of the section dealing with each group especially treated.

I. RATITAE

Although there has been some doubt concerning the natural association of all the so-called ratite birds into a single group, as far as feather structure is concerned, this grouping seems to be entirely permissible, providing the Crypturiformes, which Knowlton placed with them, be removed. The following characters are common to the entire group, and as far as we know are not present, except as noted, in the adults of any other birds: (1) plumage uniform, not segregated into pterylae (found only in Sphenisciformes and Palamedeae among carinate birds); (2) total absence of differentiated plumules and filoplumes; as far as known, both these types of feathers are never missing simultaneously in other birds; (3) entire absence of true pennaceous structure in any of the feathers,

the barbules in some species being more or less intermediate between a downy and a pennaceous type.

1. Order STRUTHIONIFORMES

Pl. 13, Fig. 2

This group, which includes only the ostriches, of which four closely related species have been described, has a great many peculiar epiphyiological characters, most of which, it seems to me, may be considered primitive, rather than secondarily acquired degenerate conditions. They may be enumerated as follows: (1) in common with other Ratitae, an even distribution of feathers, the only apterium being the central one on the breast, where there is a callosity developed by the bird's habit of resting on its breast, and the total absence of plumules and filoplumes; (2) the great increase in the number of rectrices and remiges, the latter to 36 or more, considered by Beebe (1904) to be a secondary specialization, though by some considered a primitive character; (3) the projection of the remiges beyond the bone instead of fitting into grooves in it as in all carinate birds; (4) the wide angle of insertion of the phalangeal primaries, which in other birds are attached almost parallel to the long axis of the phalanges; (5) the absence of all but one row of under wing coverts; (6) the total absence of after-shafts; (7) the total absence of a typical pennaceous structure in the feathers.

a) *Struthio camelus*

(1) *Remiges*

The feathers of ostriches, as already stated, are all of one type, and not differentiated into contour feathers, plumules, and filoplumes. The aftershaft is entirely lacking. The rectrices and remiges are developed into very large, curling plumes with loose, drooping vanes, but in their minute structure differ in no essential way from any of the body feathers.

Shafts relatively stout, usually widely and more or less deeply grooved beneath. In male wing plumes, for instance, the groove so deep and prominent as to make the shaft C-shaped in cross-section and shell-like almost to tip. Width of the shaft of a small wing plume, 6 to 7 mm. at the base, tapering gradually all the way to the end; its depth about 4 mm., 3 mm. of which is involved in the groove.

Barbs, which may reach a length of 15 or 20 cm., usually set

about 8 per centimeter on each side throughout most of the feather, increasing to about 12 or 14 at the base. *Rami* not lamellate as in most carinate birds, but more closely resembling the *rami* of down; no prominent dorsal or ventral ridges. Inner and outer vanes undifferentiated.

Barbules (pl. 13, fig. 2a) differing widely in form from those of any other birds, either ratite or carinate, at once recognizable. Not differentiated either into distal and proximal, or outer vane and inner vane types, nor any considerable difference in structure and form, except length, in different parts of feathers, or in feathers of different parts of the body. Barbules not clearly differentiated into base and pennulum, even to the extent of ordinary down barbules, and further differing from the latter in being flat and ribbonlike instead of filamentous, in this particular approaching pennaceous barbules but differing from them in being bilaterally symmetrical. On best developed barbules, no prongs or barbicels whatever, but small rudimentary prongs, as in barbules of body feathers, on weaker ones at base and tip of barbs. Length of barbules from 2.5 to 3.5 mm.; width, about 0.035 mm., this being comparable with that of pennaceous barbules; on an average about 25 to 30 barbules per millimeter on each vanule, thus more widely spaced than usual with ordinary down barbules.

(2) Other Feathers of Adult

The feathers of *back*, *rump*, *belly*, etc., not differing in any considerable degree from remiges. Barbs set closer, about 12 to 18 per centimeter throughout length of feather, usually under 5 cm. long, basal and distal ones usually shorter resulting in doubly tapering form of feathers. Barbules of approximately same form as in remiges (pl. 13, fig. 2b, 2c), those of the less well-developed feathers with rudimentary prongs at the junction of the cells, called "vestigial barbicels" by Beebe (1904). Length variable, less than in remiges, usually under 2 mm.

Feathers of *head* and *neck* small, with elongated, bare, hairlike shafts. *Eyelashes* present, in form of stiff, coarse bristles, with a few basal barbs. Specialized *ear coverts* present, similar in general plan to those of carinate birds, the shaft furnished with a series of stiff and elastic bristle-like barbs, entirely separate from each other, arranged like the tufts of a brush rather than in distinct vanes, and barbules very small, rudimentary, and appressed. In all small feathers of head and neck, including eyelashes and ear coverts, elongated, bristle-like shafts naked, but barbs always with complete series of densely set and very short barbules, only 0.015 to 0.03 mm. long, but of typical ribbon-like form.

(3) Nestling Feathers

The nestling feathers of ostriches have exactly the same type of structure of barbules as teleoptiles, which fact furnishes some evidence that the latter are not degenerated pennaceous barbules but are highly developed downy ones, since down barbules are the only ones ever found in neossoptiles. The barbules of the latter

(pl. 13, fig. 2c) differ only in their shortness, reaching a length of considerably less than 1 mm., the width and flattened ribbon-like form remaining the same. In the nestling feathers many of the barbs bear barbules only near the base, the terminal portion being extended hairlike or expanded into a more or less curled, flattened plate (pl. 13, fig 2d). Duerden (1911) gives an interesting account of the sequence in the plumages of ostriches.

b) Relationships

As has been shown, the feather structure of ostriches seems to indicate a primitive rather than a degenerate condition. Their wings, which have no specialized pennaceous remiges, and could have no lifting function, are used for aiding the bird in running against the wind, as suggested by Beebe (1904). This use is highly suggestive of a possible course of evolution of flight. When once the remiges had become pennaceous, nothing further would stand in the way of their being used for true flight. Beebe (1904) looks upon this use of the wings as a half return to the lifting function of the wings in the flying ancestors which he assumes for the group, a view which seems to me to involve so complicated a path of evolution as to require very strong positive evidence to support it. The same author remarks that "vestiges of barbicels" can easily be distinguished. He evidently considered the downy feathers of ostriches as being derived from pennaceous feathers, though nothing in their structure or arrangement, it seems to me, need be interpreted as suggesting this. The barbules, while less specialized than typical pennaceous barbules and more specialized than simple down barbules, are not intermediate, and might be more easily looked upon as marking the end of a short path of evolution of their own, than as degenerate forms of either of the other types. If the contour feathers of ostriches are *not* derivatives of pennaceous feathers, then ostriches are not descendants of flight birds, and their striking primitive characters need not be looked upon as secondarily acquired. The absence of plumules, filoplumes, and aftershafts, the even distribution of feathers over the entire body, and the similarity of the neossomptiles to the teleoptiles, as well as the general form of the barbules, all suggest the possibility of the ostriches not being derived from birds with pennaceous feathers, and therefore not from flight birds.

c) Summary

The ostriches, in addition to the characters common to all Ratitae, have the following characters:

(1) Aftershaft absent.

(2) Types of barbules similar on all feathers of both nestling and adult.

(3) Barbules of elongate, ribbon-like form, more or less intermediate between an ordinary downy and a pennaceous type, but different from either, with no differentiation of base and pennulum, and no barbicels except rudimentary prongs in body feathers.

(4) Possibility of their not being derived from flight birds strongly suggested by epiphylogy.

2. Order RHEIFORMES

Pl. 13, Fig. 1

Although grouped as a separate order of the Ratitae, equivalent to any of the other three, the rheas are much more closely related to the ostriches than are either to any others of the Ratitae, especially as regards their epiphylogy.

Rheas agree with ostriches, in addition to the common ratite characters, in (1) the large number of primaries (12 to 16 in *Rhea*), (2) the reduction of the under wing coverts, they being totally absent in *Rhea*, (3) the absence of aftershafts, and (4) the type of barbules, which, as in ostriches, are intermediate between downy and pennaceous barbules. The chief differences between the two groups in general epiphylogologic characters are: (1) the absence of well-developed rectrices in *Rhea*, (2) the more obtuse angle made by the attachment of the phalangeal primaries in *Rhea*; (3) the approach to the carinate type of the relation of the remiges to the arm bones; and (4) the better development of the feathers of the head and neck.

The details of structure of the feathers, as compared with ostriches on the one hand and carinate birds on the other, are exceedingly interesting.

*a) Rhea americana**(1) Remez*

Shaft, unlike its condition on some ostrich feathers, finely ridged and grooved on ventral side, with no large conspicuous groove in middle. As a rule, the shaft not as short or heavy relative to feather as in ostriches.

Barbs very similar to those of ostriches, with no perceptible ventral or dorsal ridge, and with barbules attached almost at right angles in an even series almost directly opposite each other, and not at obviously different levels as in pennaceous feathers. Change in number of barbs per unit of measure from base to tip of feathers considerable; about 20 per centimeter at base of feather, diminishing to only 8 or 9 near tip.

Inner and outer vanes similar. *Barbules* considerably advanced over those of ostriches in their greater variability in different feathers and parts of feathers, also in their closer approximation to both a pennaceous and downy type. Set about 35 per millimeter on each side on basal barbs, and only about 20 per millimeter on terminal ones. No differentiation between distal and proximal barbules. The best developed barbules on basal portion of barbs on terminal halves or remiges (pl. 13, fig. 1a). Length about 2 mm., the basal one-third, more or less, considerably broadened into specialized base, not bilaterally symmetrical, but furnished with a series of ventral prongs or barbicels, the dorsal edge smooth and unbroken. Pennulum cylindrical, with more or less well-developed prongs for its entire length. Development of basal portion into a differentiated unsymmetrical base, with distinctly barbicel-like prongs, and of terminal portion into a filamentous pennulum, shows distinct approximation to pennaceous barbules, at least much nearer than the simple, ribbon-like barbules of ostriches.

Barbules from middle part of either vane of same feather (pl. 13, fig. 1c) considerably less specialized. Basal portion much narrower with less distinct barbicels, and a much less obvious distinction between flattened base and filamentous pennulum.

(2) Other Feathers

No essential differences from remiges in structure of *body feathers*, but barbs more numerous. On small rump feather they decrease from 40 per centimeter on each side at base to about 22 at tip, in upper back feather less numerous, 30 per centimeter basally to about 13 at tip. In these cases number of barbs per unit of measure apparently increases inversely to size of feather, or, in other words, space between barbs is directly proportional to size of feather. Barbules less differentiated into base and pennulum than in remiges (pl. 13, fig. 1b), and shorter, with decided tendency toward ordinary downy type, similar to that of penguins, and to neossoptiles of many water-birds.

I have had no opportunity to study neossoptiles of rheas, but they are stated by Gadow (1891) to be "buschelformig" as in ostriches, but with a weakly developed shaft.

b) Relationships

Like the Struthioniformes, the rheas show characters which might be construed as evidence of their being primitive in their flightless condition and of not being descendants of flying birds.

As shown above, they resemble the ostriches in many details, and are unquestionably more nearly related to them than to any other Ratitae. In the general arrangement of feathers and in the form of the barbules, while probably, like ostriches, at the end of a short separate path of evolution, they appear to be nearer the line of descent of carinate birds. Special attention is drawn to the fact that the barbules which approach most nearly a pennaceous type, are in the positions where pennaceous barbules are most likely to be found at the height of their development in carinate birds, i. e., on the basal portion of barbs beyond the middle of the feather.

c) Summary

In addition to common ratite characters, Rheiformes are characterized by the following in common with ostriches:

- (1) Absence of aftershafts.
- (2) No under wing coverts (one row in ostriches).
- (3) Unusually large number of primaries.
- (4) A type of barbule which is intermediate between a downy and a pennaceous type, differing, however, from ostriches.

They are further characterized by:

- (1) Differentiation of the barbules of different portions of feathers.
- (2) Highest developed barbules with flattened base provided with barbicels on ventral edge only, and filamentous pennulum with prongs similar to those of typical down feathers of penguins.
- (3) Less highly developed barbules with basal portion reduced, thus becoming still more like the down barbules of penguins.

3. Order CASUARIFORMES

Pl. 14, Figs. 3, 4

The birds of this group differ very considerably from the ratite birds previously studied, but agree with them in the several important characters common to all ratites. Although Nitzsch (1867) described filoplumes from a cassowary, he was undoubtedly mistaken in his identification of them (see Part I, p. 260), for filoplumes are as completely absent in this group as in any of the other Ratitae. Unlike those of the ostriches and rheas, the primaries are greatly reduced, hardly differentiated at all in Dromaeidae, and reduced to five or six stiff black spines in Casuariidae, representing, according to Beebe

(1904), only the hypertrophied calami, the scanty-vaned shaft being first formed and then broken off at the superior umbilicus. No specialized rectrices are to be found. The aftershaft is enormously developed, nearly or quite equalling the main feather plate, a condition found elsewhere only in plumules and in the ear coverts of some birds.

The plumage of these birds differs widely from that of the ostriches and rheas in being very hairlike and harsh to the touch, a condition brought about by the looseness of the vanes, and the stiffening of the rami, coincident with a reduction and loss of the barbules.

a) *Dromaeus novae-hollandiae*

(1) *Body Feathers*

Body feathers characterized by great slenderness of form. *Feather plate* extremely long relative to width; total length in a typical, back feather of both shaft and aftershaft, about 20 to 25 cm.; width approximately uniform for entire length, less than 1.5 cm. wide; feather slightly rounded at tip. *Aftershaft* not appreciably different. *Shaft* slender, slightly more so in aftershaft, with a broad, shallow, ventral concavity. *Rami* typically of rather peculiar form, especially towards tip of feathers, where in many feathers the barbules are more and more restricted to basal portion of barbs and finally lost entirely. These naked terminal barbs set as close together as are the middle, barbuliferous ones (about 8 or 9 per centimeter), with rami very deep dorso-ventrally, and sword-shaped, dorsal edge wide and smooth like the upper edge of a sword blade, lower edge thin and sharp, tapering up to meet the upper edge at tip (pl. 14, fig. 4a). Rami of more proximal barbs, bearing barbules, similar but not so wide or so evidently sword-shaped.

Barbules alike on inner and outer vanes, usually present to tips of barbs on at least two-thirds of feather, and sometimes to tip of feather; about 1 to 1.8 mm. long, very slender, and very numerous, set about 30 to 35 per millimeter on both sides. Unlike those of ostriches and rheas, barbules of typical downy type, with narrow, flattened base, and long, filamentous pennulum (pl. 14, fig. 4b). Base short, of moderate width, pennulum almost absolutely thread-like, the nodes very inconspicuously marked by minute prongs. All barbules from either aftershaft or main feather plate, and from all feathers examined, similar in form, differing only in size.

b) *Other types. Casuariidae*

Though very much like the emus in all the important characters of their epiphylogy, cassowaries differ in a few minor details. A much larger proportion of each feather is composed of naked shaft and rami, and the latter are widely separated from each other, not

forming compact, well-developed vanes, the result being that the plumage of these birds is much coarser and more bristly than that of emus.

The feathers have a somewhat different general shape. While in emus they are elongate and narrow with approximately a uniform width throughout, in cassowaries their widest point is a few centimeters above the umbilicus, thence more or less gradually tapering to the tip. The aftershaft is as highly developed as in emus, and as with the latter resembles the main feather plate in structure as well as size. The calamus is exceedingly short, shorter in *Casuaris uniappendiculatus* than in *C. papuanus*; in fact, it is so short in the former that the division into shaft and aftershaft occurs under the surface of the skin, the feather thus appearing completely double. The barbs are moderately developed, not sword-shaped, and spaced about 7 or 8 per centimeter, increasing to 16 per centimeter at the base; the barbules (pl. 14, figs. 3a, 3b) are of about the same length as in *Dromaeus* (1 to 1.8 mm.) but entirely lack the prongs at the nodes, the latter being indistinguishable, and the pennula simple threads. The naked terminal portion of the feather, which sometimes constitutes three-fourths of the entire feather, and reaches a length of over 20 cm., sometimes has the stiff, bristle-like naked barbs present in decreasing numbers all the way to the tip, where there are only two or three per centimeter on each side, while in other cases, especially in shorter feathers, the naked shaft is produced as a very coarse, stiff bristle.

c) Relationships

While agreeing with the ostriches and rheas in characters common to all the Ratitae, the cassowaries and emus differ from either of the former types far more than they differ from each other. The present group, with the Apterygiformes, on the one hand forms a subdivision of the Ratitae comparable with the Struthioniformes and Rheiformes on the other, though the latter are more nearly related to each other than are the former. The enormous aftershaft, the few reduced remiges, the coarse texture of the plumage, and the form of the barbules, are all striking points of difference from the ostriches and rheas, while in all except the aftershaft they agree more closely with the Apterygiformes in these characters. Although in their feather structure there is no positive evidence of their being primitively rather than secondarily flightless, there

is positive evidence favoring this theory in the ostriches and rheas, as already shown, and the evident close relationship of the latter birds to those of the present group is a strong argument in favor of the Casuariiformes not having had flying ancestors.

d) Summary

The Casuariiformes have the following characters in addition to those common to the ratites:

(1) Remiges greatly reduced, functionless in Dromaeidae, their calami developed into a few stout spines in Casuariidae;

(2) Texture of plumage coarse and hairlike, due to long, narrow feathers which have more or less of terminal portion composed of a coarse shaft and rami with no barbules;

(3) Aftershaft similar to main feather plate in both size and structure;

(4) Barbules of downy type, practically invariable on different parts of the body, the bases narrow and flattened, the pennula long and filamentous, with prongs sometimes developed at the nodes in *Dromaeus*, none whatever in *Casuarius*.

4. Order APTERYGIFORMES

Pl. 14, Fig. 5

This group, comprising several species of a single genus, is probably the nearest to the carinate stem of all the ratite birds. Their general epiphylogenical characters are as follows: (1) the presence of small lateral apteria, as well as a ventral one (Parker 1891); (2) absence of differentiated plumules and filoplumes; (3) remiges and rectrices rudimentary and functionless; (4) aftershaft entirely absent; and (5) no pennaceous structure present.

The minute structure of the feathers comes nearer to the down of the carinate birds than it does in any other ratite birds. No specialized remiges are present and all the feathers are very similar.

a) *Apteryx haasti*

(1) Body Feathers

Shaft and *calamus* both slender, the former with no discernible ventral groove, and tapering evenly for greater part of its length, widening out a little terminally to produce a stiff, coarse tip.

Vanes tapering in both directions from about one-third of distance from calamus to tip of feather. At widest point *feather plate* about 3 cm. wide, total length seldom over 10 cm., thus giving feather a much wider form than in case of *Casuariiformes*. *Barbs* 14 per centimeter on each side basally, only 9 or 10 towards tip of feather, set at right angles to shaft on lower part of feather, the angle gradually becoming more acute toward tip, so that even though barbs are actually considerably longer, the vanes taper evenly. Barbs on basal part of feather furnished with barbules for whole length, but towards tip barbiferous portion more and more restricted to basal portion of barbs, the terminal parts of which are elongated into moderately slender, black hairs lying close to each other, and with totally different appearance from the bare, coarse barbs of cassowaries and emus. *Barbules* very slender and filamentous, of typical downy type. Base short, but well-formed, about 0.017 mm. wide. Pennulum 0.008 mm. in diameter, varying from perfectly smooth filament in basal barbs to filament with distinct nodes and minute prongs in more terminal barbs (pl. 14, figs. 5a, 5b). In well-developed downy region of vanes, barbules from 2 to 3 mm. in length, set 25 to 35 per millimeter, but in more terminal portion, where reduced, diminishing greatly in length, but concomitantly stouter, with more distinct prongs.

Little variation in structure in different feathers. Around base of bill a few long, hairlike rictal bristles developed, formed by greatly elongated shafts of minute facial bristles.

b) Relationships

Apteryx apparently has a peculiar mingling of primitive, specialized, and degenerate characters, but, as hinted under *Casuariiformes*, its feather structure suggests a rather closer affiliation to the *Casuariiformes* than to any other birds, and it seems best to regard the genus as an early offshoot from the stem leading to the latter group.

The presence of vestigial (rudimentary?) apteria in these birds has been considered by many authors as indicative of their descent from a type possessing well-formed apteria, but it seems to me that there is fully as much ground for looking upon this feature as a beginning rather than a vestige. As in the case of other ratite birds, the absence of differentiated plumules and filoplumes is much more easily thought of as a primitive than as a degenerate character. The remiges and rectrices may have been better developed in their ancestors, but there seems to be no positive ground for believing that they ever possessed lifting power. The absence of the aftershaft may be a primitive or a secondarily acquired character. Its absence is the chief epiphyiological divergence from the *Casuariiformes*.

c) Summary

In addition to the common ratite characters, Apterygiformes are characterized by:

- (1) The presence of small apteria;
- (2) No specialized remiges or rectrices;
- (3) No aftershaft;
- (4) Feathers broad and tapering, outer part of barbs naked towards tip of feather;
- (5) Barbules of typical downy type, smooth and filamentous, or with distinct nodes and prongs on pennulum, the base small but well-formed.

5. SUMMARY OF RATITAE

Based on epiphylogeny the Ratitae are divisible into two main groups, the Struthioniformes and Rheiformes on the one hand, the Casuariiformes and Apterygiformes on the other. All of them agree in the absence or rudimentary condition of the apteria, the uselessness of the remiges for flight, the absence of differentiated plumules and filoplumes, and the lack of any typical pennaceous structure.

The first group seems to represent two branches of an early offshoot from the stem leading to carinate birds, the type of feather structure being at the end of a short path of evolution, the barbules in both cases differing from either a pennaceous or downy type, but apparently not leading to either. The aftershaft is absent in this group.

The second group seems to represent two branches of another but possibly later offshoot from the carinate stem, the barbules being of typical downy type, and resembling, especially in Casuariiformes, the down barbules of penguins and of the neossoptiles of many other forms of water birds. In the Casuariiformes the aftershaft is equivalent to the main feather plate; in Apterygiformes it is absent. In the latter group small lateral apteria are present, but there is as much reason to believe them to be just developing as to look upon them as vestigial.

II. CARINATAE

All of the birds included in this group differ from those already considered in the following important details: (1) the presence of apteria in all but the Sphenisciformes and Palamedeidae; (2) the presence, or undoubtedly secondary loss, of plumules and filoplumes; and (3) presence in the adult of both downy and pennaceous structures, while the nestling feathers are always downy.

1. Order SPHENISCIFORMES

Plate 15

The epiphylogy of this group differs widely in a number of points from that of all other living birds. With the sole exception of the Palamedeidae, they are the only carinate birds with an absolutely uniform distribution of feathers, the contour feathers and plumules both being evenly distributed over the entire body. No specialized remiges are developed and it seems probable that the first row of feathers on the posterior margin of the wing is not homologous to the remiges of other birds, but represents the under wing coverts, the third row of feathers representing the true remiges; this interpretation is based on the fact that in these birds there are no under wing coverts with a reversed position (i. e., umbilicus exposed), as there are in all other birds (Wray, 1887a). The rectrices are represented by a row of feathers which have the shaft very stiff and spine-like, with relatively short, stout, appressed barbs, and weak, reduced barbules.

a) *Aptenodytes pennanti*(1) *Body Feathers*

Details of feather structure very distinct from that of birds of any other group. *Calamus* cylindrical and transparent, constricted at superior umbilicus, where it gives off the shaft and an *aftershaft*. The shaft of latter sub-triangular, about 0.1 mm. wide at junction with calamus, widening out to about 0.4 mm. in the 2 mm. of its length, then giving off a large number (50 or more) of very delicate, downy barbs about 1.5 cm. long in feather about 4 cm. long. Down of aftershaft like that of main feather plate, except barbules shorter.

Shaft remarkably broad and flat, in feather under consideration about 2.5 mm. wide a short distance distal to superior umbilicus, considerably under 1 mm. in depth, tapering gradually to tip; very flat, only slightly convex above and below, a slight median ridge on each surface. *Rami* attached to narrow edge of shaft, thus not nearer

dorsal surface as in other birds. *Barbs* very numerous, about 30 or 40 per centimeter on each side, thus in some measure making up for weakness of structure by strengthening vanes. More or less of inner portion of barbs, usually about one-half, furnished with primitive pennaceous barbules; outer portion downy, compactness of vanes being maintained only by stiffness of rami. Terminal portion of feather devoid of barbules, rami becoming cylindrical and bristly.

Inner and outer vanes similar. *Distal barbules* of pennaceous portion (pl. 15, figs. 6a, 6b) with poorly developed base. Pennulum with a series of ventral barbicels extending to tip, not differentiated into ventral teeth, hooklets, and cilia. Usually all of them much curved and hooklike, but not hooked merely at tip as in other birds. *Proximal barbules* (pl. 15, figs. 6c, 6d) with no bend or sharp differentiation between base and pennulum, the latter distinguishable only by presence of outward-curving, dorsal and ventral barbicels, which hardly differ in form from prongs of down barbules, though usually longer. Distal barbules reaching length of about 0.35 mm., the proximals about 0.6 mm., the base in each case occupying about half total length.

2. Down

Transition from pennaceous to down barbules simple and easy, the hooked form of barbicels of distal barbules being lost and size of those of proximal barbules reduced. Typical *down barbules* (pl. 15, fig. 6e, and pl. 34, fig. 96) characterized by unusual shortness, not exceeding 0.8 mm. in length, and usually considerably less. Base very narrow and poorly differentiated from pennulum. The latter naked and filamentous basally, but furnished with comparatively long and conspicuous prongs towards tip. As usual in typical down, barbules inserted in four instead of two rows, those of either side alternately projecting in different directions (pl. 15, fig. 6e). Counting all four rows, there are about 60 barbules per millimeter.

b) Other Types

The dark feathers of *Eudytes chrysocome* are very familiar, differing chiefly in having longer pennaceous barbules (pl. 15, figs. 7a, 7b), which have a dark pigment segregated into transverse bands, as in the feathers of gulls and some pigeons. This probably accounts for the bluish tinge which the feathers of this species have. In *Spheniscus mendiculus* the distal barbules are relatively short, while the proximals are long, with a well-developed series of ventral baricels; they are about 0.25 mm. and 0.68 mm. long respectively.

The stiff, spinelike rectrices of the latter species have a broad, shallow concavity on the ventral side of the shaft, although in the body feathers the shaft is very thin and almost perfectly flat both above and below.

c) Relationships

The Sphenisciformes must undoubtedly be considered the lowest of living aquatic birds, although some of their apparently primitive characters may be due to degeneration. The uniform distribution of feathers, the absence of specialized remiges and of under wing coverts with a reversed position, and the simple structure of both their pennaceous and their downy barbules, all point to their low systematic position. The broad, flattened form of the shaft, and general scale-like appearance of the feathers on the other hand are specialized characters. The most logical interpretation is to look upon them as derivatives of the extinct, aquatic, toothed birds, highly modified by specialization and degeneration for aquatic life.

d) Summary

The penguins have the following characters: (1) uniform distribution of both plumules and contour feathers;

(2) So far no filoplumes discovered;

(3) No specialized remiges, and no reversed under wing coverts;

(4) Aftershaft present, its shaft reduced, and the barbs spreading out tuftlike;

(5) Main shaft very broad and flat, usually with no ventral groove;

(6) Distal barbules very small with a weak base and a series of hooked barbicels on pennulum, these barbicels not differentiated into ventral teeth, hooklets, and cilia;

(7) Proximal barbules small but longer than distals, no distinct bend or distinction between base and pennulum except the presence of simple forward-curving ventral and sometimes also dorsal barbicels;

(8) Down barbules relatively very short, with a poorly differentiated base, and a filamentous pennulum furnished with well-developed prongs, especially toward the tip, where they are always larger.

2. Order COLYMBIFORMES**Plate 16**

The loons and grebes, which comprise the present order, though differing from each other in some details of structure, are very similar as regards their epiphylogogy. Unlike any of the preceding birds, they have well-developed apteria, and possess typical func-

tional remiges, although the birds are adapted for aquatic life. They also possess typically developed pennaceous barbules. The aftershaft is present with a short weak shaft, and numerous spreading barbs.

a) *Gavia immer*

(1) *Remes*

Development very high, totally different from primitive condition in penguins. *Shaft* slightly broader than deep, distinctly quadrangular, with narrow median groove on ventral side and barbs attached nearer dorsal surface, as in all other flight birds. *Rami* of both vanes, though narrow at junction with shaft, immediately become very wide, with a broad, membranous ventral ridge, the total width of ramus then equivalent to that of shaft, i. e., about 1.6 mm., the translucent ventral ridge constituting approximately one-fourth the width of the ramus. *Rami* taper rapidly and become narrow. Lower edge of ventral ridge almost if not quite smooth, no villi projecting ventrally. About 20 barbules per centimeter, usually a few less on outer vane, a few more on inner.

Inner vane.—*Distal barbules* (pl. 16, fig. 8a) characterized by a broad, well-formed base about 0.27 mm. long, narrowing proximal to ventral teeth; latter 1 or 2, narrow and fingerlike; pennulum moderately long; hooklets 4 or 5, moderately long and slender, well-formed; ventral cilia moderate, straight, more or less appressed to shaft; basal two or three dorsal cilia stout and triangular, the transition to rudimentary distal ones gradual. Total length of barbule about 0.6 mm. *Proximal barbules* (pl. 16, fig. 8b) rather stout, about 0.43 mm. long by 0.05 mm. wide, with about 4 long, slender, conspicuous ventral teeth; pennulum filamentous, with rudimentary barbicels.

Outer vane.—*Distal barbules* (pl. 16, fig. 8c) with elongated base (0.33 mm. by 0.033 mm.) with 2 rather small ventral teeth. Hooklet region of pennulum very broad (pl. 16, fig. 8c, this barbule being twisted to show this characteristic). Hooklets considerably increased in number, 6 or 7 present; ventral cilia very much as in inner vane, and dorsal cilia absent entirely. Towards inner part of barbs, bases of barbules much shorter and hooklets gradually changing over to curved ventral cilia, strongly hooked, reminiscent of those in penguins. *Proximal barbules* of distal part of outer vane (pl. 16, fig. 8d) with considerably narrower bases than those of inner vane, and pennulum with a complete series of ventral cilia, the more proximal ones strongly curved and hooked. The more basal proximal barbules very similar to those of inner vane, the ventral teeth elongating on more distal barbules, ultimately forming the 4 or 5 proximal hooklike ventral barbicels, the more proximal cells of pennulum adding more barbicels to these until a complete series is formed.

(2) *Other Feathers*

Back feathers with well-developed interlocking vanules basally. Distal barbules with both base and pennulum elongated, the former

with single, slender ventral tooth, the latter with 3 or 4 short hooklets, and a series of curved ventral barbicels. Type same as that in *Aechmophorus occidentalis* (pl. 16, fig. 9e). Proximals with slender, elongate base, and slender pennulum, the latter with a series of moderate ventral barbicels. See plate 16, figure 9f (*Aechmophorus occidentalis*). On distal portion of feather, both distal and proximal barbules reduced to single elongate type, resembling somewhat proximal barbules of penguins; no sharp demarcation between base and pennulum, but latter with a series of curved ventral barbicels; base, on some of terminal barbules, with one or two flexules developed (pl. 16, fig. 9g, of *Aechmophorus occidentalis*), a highly significant fact considering their universal occurrence in *Procellariiformes*.

Breast feathers well-developed, with fairly strong vanes. Barbules remarkably similar to those of penguins; distals (pl. 16, fig. 8e) with narrow base and weak ventral teeth, pennulum with long series of short hooklets, gradually changing to curved ventral cilia, exactly as in penguins; proximal barbules towards tip of barbs (pl. 16, fig. 8f) with slender tapering base and barbicelled pennulum, the ventral cilia longer than dorsal, but both series present.

b) Other Types

Gaviidae.—*Gavia pacifica* has practically identically the same structure as the species above described.

Colymbidae.—In *Aechmophorus occidentalis* the structure of the remiges is strikingly similar to that of *Gavia*, differing only in a few details. The rami are not so deep and have not so wide a ventral ridge as in the *Gaviidae*, and they are set closer on the shaft, there being about 25 and 28 per millimeter on the inner and outer vanes respectively. The barbules are essentially the same in structure as in *Gavia*, but, as would be expected on smaller feathers, they also are smaller; the distals (pl. 16, figs. 9a, 9c), for example, are only about 0.47 mm. long, the base constituting about half of this. On the proximal barbules of the inner vane (pl. 16, fig. 9b) the base is relatively longer and narrower, with less conspicuous ventral teeth, while in the proximals of the outer vane (pl. 16, fig. 9d) the barbicels are much smaller and weaker. *Colymbus holboelli* and *Podilymbus podiceps* are similar, but the barbicels of the proximal barbules of the outer vane are still less conspicuously developed, and confined to barbules on a less extensive portion of the barb.

The back feathers of *Aechmophorus occidentalis* closely resemble those of the loons. In most other grebes, however, e. g. the various species of *Colymbus* and *Podilymbus*, a hairlike effect is produced in

the plumage by the wearing away of the barbules on the exposed portions of the barb.

The breast feathers of the Colymbidae differ very considerably from those of the Gaviidae. In *Aechmophorus occidentalis* the breast feathers are exceedingly dense, inserted perpendicular to the contour of the body, with the terminal portion sharply turned to lie flat on the contour, this arrangement resulting in an unusually dense plumage. The feathers are peculiar in having the barbs set conspicuously wide apart on the shaft, about 13 per centimeter, and set at rather a wide angle. The barbules are set about 20 per millimeter on each side, and are about 0.75 millimeter in length. They are of a very unusual type, flattened for about half their length and then filamentous, the flattened portion being spirally twisted. There is a further complication in that only every second, sometimes every third, barbule reaches across to the neighboring barb, the intervening ones being twisted so as to lie nearly parallel to the barb and ventral to it (pl. 16, fig. 9h). On the outer portion of the more distal barbs this peculiar structure is lost and the barbules become elongate (over 1 mm.), slightly flattened, and less twisted, and develop on their distal ends a double series of barbicels, the ventral ones curved and hooklike, exactly similar to the barbicels of the distal barbules in penguins. At the same time the barbs and barbules become ribbed in such a way as to become strongly reflective, and they give a shiny, silky appearance. The result of this peculiar structure is a very much curved, loose, open-vaned feather, which in the aggregate gives the thick silky breast so characteristic of grebes. Various species of *Colymbus* and *Podilymbus* show precisely the same structure.

c) Down

The down of loons (Gaviidae) very closely resembles that of penguins, being very short, usually under 0.5 mm., and with well-developed prongs, exactly as in penguins. In grebes the down is considerably longer, often considerably over 1 mm. long, and frequently with the prongs very slightly developed.

d) Relationships

As will be seen from the above descriptions, the feathers of grebes and loons are very highly specialized and differentiated, and

show an almost perfectly intermediate position between penguins on the one hand and Procellariiformes on the other. In the structure of the breast feathers and down, loons come much nearer the Sphenisciformes than do grebes, and they are also more similar to the Procellariiformes. The grebes appear to represent a separate offshoot of the group, and have a condition of the breast feathers which is different from that of any other birds except some of the Alcidae.

e) Summary

Colymbiformes are characterized as follows:

- (1) Aftershaft present, its shaft short, and barbs spreading;
- (2) Distal barbules of inner vane of remiges with small, slender, ventral teeth, moderate hooklets and ventral cilia, and stout, triangular, proximal dorsal cilia;
- (3) Distals of outer vane with elongated base, the hooklet region of pennulum broad, and a considerable increase in number of hooklets;
- (4) Proximal barbules with rather well-developed, slender ventral teeth on inner vane and a series of hooked barbicels on outer;
- (5) Breast feathers characterized by peculiar twisted barbules in Colymbidae, but very reminiscent of Sphenisciformes in Gaviidae;
- (6) One or two flexules appearing on terminal barbules in breast feathers;
- (7) Down barbules short, strikingly similar to those of the Sphenisciformes.

3. Order PROCELLARIIFORMES

Plate 17

The albatrosses, petrels, puffins, and other birds that comprise this order form a very well-marked and easily recognizable group, and it is not surprising to find that they possess a number of constant epiphylogenic characters. The plumules are evenly distributed over the whole body, between the contour feathers and in the apteria. The wing is very long in some species, due to the large number of secondaries, these varying from 10 to 37 in different species. The aftershaft is present, though sometimes very weak and vestigial. When well-developed, e. g., in *Oceanodroma*, its shaft is short and the barbs spread out in a tuft as in the Colymbiformes. In *Diomedea* it is very minute, while in *Pelecanoides* it

is over half the length of the main feather plate, with 30 or more barbs in the breast feathers.

a) *Diomedea exulans*

(1) *Remes*

Highly specialized as functional flight feather, the barbules in fact possessing more "frills" than in any other feather known. Shaft deeper than wide, especially on more proximal portion of feather, with sharp, inconspicuous groove; calamus large and inflated. Vanes firm and elastic; barbs fairly close together, about 18 per centimeter on inner vane, somewhat less on outer, their rami considerably deepened near junction with shaft, and barbules firmly interlocking. Pith of barbs consisting of only a single layer of hollow cells transversely, the ventral ridge not as broad and thin as in loons, but constituting about a fourth of depth of barb.

Inner vane.—*Distal barbules* (pl. 17, fig. 10a) with a number of rather striking characteristics. Twist between base and pennulum unusually pronounced, making a very sharp curve in dorsal contour of barbules as they lie undisturbed in vanule. Base large and rather long, 0.45 mm. by 0.16 mm., differing from barbs of birds of any other group, as far as known, by the presence of one or two minute forward-projecting prongs on dorsal edge, on cells bearing ventral teeth. Latter very peculiar in form, not simple finger-like or lobate projections, but bifid at tip, and often trifid (pl. 17, fig. 10a). Pennulum longer than base; hooklets moderate and well-formed; ventral cilia long, slender and flexible; the dorsal cilia with much the same character as in Colymbiformes, i. e., short and triangular basally, then becoming more slender, and finally decreasing, those beyond the sixth usually rudimentary or absent entirely. *Proximal barbules* (pl. 17, fig. 10b) large and well formed; base very long and relatively slender; about 0.76 mm. by 0.06 mm. with a well-developed flange, and rather small dorsal spines; ventral teeth differing from those of all other birds in being slender, flexible, and greatly elongated, sometimes 0.15 mm. long, and usually with wavy appearance, as shown in figure. Pennulum approximately equal to base in length, broad at proximal end (about 0.01 mm.), tapering gradually to tip. Distal barbules set very close together, about 30 per millimeter, proximals, being set at a much more acute angle, much less numerous, about 17 per millimeter.

Outer vane.—*Distal barbules* (pl. 17, fig. 10c) differing from those of inner vane in same manner as in loons, i. e., base slightly more elongate, hooklet region of pennulum broader, hooklets more numerous, ventral cilia longer and more filamentous, and dorsal cilia undeveloped except terminally, but specific characteristics, such as dorsal prongs and jagged ventral teeth, unchanged. *Proximal barbules* (pl. 17, fig. 10d) with shorter and more tapering base, and extremely long, heavy pennulum with a complete series of ventral barbicels, the more proximal of which long and wavy,

the more distal ones shorter and not so delicate, often more or less appressed to the shaft; towards tip dorsal cilia also developed. Pennulum 1 mm. or more in length, 0.01 mm. wide.

(2) Other Feathers

Secondaries differ from primaries in having pennula, especially of distals, greatly increased in length, like the pennula of proximals of outer vane of primaries. *Back feathers*, near base of barbs, with distal barbules almost identically like those of inner vane of remiges, but with pennula longer, and dorsal barbicels weaker. Proximals, like those of outer vane of remiges, having very long, heavy, barbicelled pennula towards tip of barb, but only 4 or 5 slender, wavy teeth on more basal part of barb. On distal portion of barb, i. e., approximately distal third, flexules developed on distal barbules, but transformation of barbules slight as compared with breast feathers.

In *breast feathers* proximal portion of barbs not materially differing in structure from that of back feathers, except that barbules are weakened and the characteristic features less distinct. Terminal portion of barb, however, entirely transformed. Distal barbules (pl. 17, fig. 10e) with a series of flexules continuous with dorsal pennular series of barbicels except in hooklet region; base narrow, and no marked bend between base and pennulum. As shown in figure, all barbicels, even hooklets, have tendency to bifurcate. Proximal barbules also develop flexules, becoming similar in form to that in *Oceanodroma melania* (pl. 17, fig. 12b).

b) Other Types

In *Puffinus griseus* the structure of the remiges is very similar to that of *Diomedea*. All barbules, as shown in plate 17, figures 11a-c, though smaller, and with the characteristic features less conspicuous, nevertheless differ in no essential points. The back feathers of this species have the characteristic details of structure still less distinct, the dorsal prongs and dorsal cilia of the distal barbules, and the wavy form of the ventral teeth of the proximals, being undeveloped. The breast feathers have the same structure as in *Diomedea*.

Oceanodroma melania has the minute structure of the remiges very much like that of *Puffinus*, though the barbules, of course, are smaller, the base being about 0.3 mm. long, (relatively very large, except in this order) and with the same conspicuousness of the twist at the junction of the base and pennulum, but the dorsal prongs of the base are exceedingly minute or missing entirely. In all other details, the structure is essentially the same as in *Diomedea* and *Puffinus*.

The back feathers of *Oceanodroma melania* have a weak struc-

ture as compared to those of the species already described. The distal barbules for the greater length of the barbs have well-formed bases with no flexules, only two or three weak hooklets, and no dorsal cilia. The proximals, at the base of the feather, have only two small, inconspicuous ventral teeth, but acquire four long and slightly wavy ones farther distad on the barb. Near the tip of the barbs the flexules are developed, beginning nearest the penulum instead of at the proximal end of the base, the latter becoming narrow and reduced, concomitant with the development of the flexules. This is well shown in plate 17, figures 12a and b.

In *Pelecanoides urinatrix*, belonging to the genus which may be regarded as the least specialized member of the group, the *breast feathers* have the barbules for the greater part of the barb weak, but of ordinary type, i. e., without flexules. The bases of the distals are narrow and elongate, the ventral tooth, usually single, very small and simple, and the pennula hardly longer than the base, slender, with usually only two weak hooklets; a series of short ventral cilia similar to those of the body feathers of loons (pl. 16, fig. 8e). The proximals do not possess the elongate, wavy ventral teeth so characteristic of the more specialized members of this order, but have these structures so small and inconspicuous as hardly to be discernible at all. Near the tip of the barbs the same sort of a change takes place that occurs in *Oceanodroma*, i. e., a development of flexules with an accompanying reduction of the base, the ventral cilia being still well developed. The similarity of this type of barbule to those developed at the tip of the barbs of the breast feathers of loons seems highly significant. This resemblance is strongly brought out by a comparison of plate 17, figure 12b, with plate 16, figure 8f, representing the barbules of the tip of barbs of breast feathers of *Oceanodroma* and of *Gavia* respectively.

c) Down

The down barbules in *Diomedea* and *Puffinus* (pl. 34, fig. 97) are characterized by rather long, forward-curving prongs which are slender and cilia-like in form, sometimes nearly 0.04 mm. long and not infrequently forked. They are longest near the base of the barbule, decreasing to rudimentary prongs toward the tip. The total length of the barbules sometimes reaches 1 mm., but is usually somewhat less.

In *Oceanodroma* and *Pelecanoides* the barbules are slightly shorter, usually 0.8 to 0.9 mm. long, and have very small prongs, not noticeably larger near the base of the barbules than at the tip. The black pigment in the case of *Oceanodroma melania* is evenly distributed in the barbules, or almost so.

d) Relationships

The Procellariiformes, in the structure of their feathers, show unmistakable resemblances to the Colymbiformes, especially the loons, so much so that their close relationship can hardly be doubted. They show, however, a considerably higher degree of development than do the Colymbiformes, the barbules of both remiges and body feathers possessing all the ordinary types of barbicels in highly developed form, as well as some special structures of their own. The bifurcated ventral teeth, dorsal prongs on the base in the distal barbules of the remiges, and the elongated, delicate, wavy ventral teeth of the proximals, are characters belonging solely to Procellariiformes, or at least reach their highest development there. The flexules of the body feathers also reach their highest development in these birds. In view of these facts, we must look upon the Procellariiformes, at least the more specialized ones, such as *Diomedea*, as representing the end of a path of evolution of their own, while a more primitive procellariiform bird probably gave rise to the Ciconiiformes through the Steganopodes (see page 315).

e) Summary

Procellariiformes may be characterized as follows:

- (1) Plumules evenly distributed;
- (2) Aftershaft present;
- (3) Distal barbules of inner vane of remiges with minute dorsal prongs on cells bearing ventral teeth (undeveloped in *Pelecanoides*), the ventral teeth bifurcated or jagged, ventral cilia well developed, slender and flexible, and the basal dorsal cilia triangular, gradually becoming slender;
- (4) Distals of outer vane of remiges differing in having more slender base, hooklet region of pennulum wider, hooklets more numerous, and basal dorsal cilia absent;
- (5) Proximals of inner vane of remiges with very long slender base, with elongated, delicate, wavy ventral teeth, and with pennulum stout basally;

(6) Proximals of outer vane with tapering base, and very long, heavy pennulum, with slender, wavy, or curved barbicels basally, and usually both dorsal and ventral barbicels on greater part of its tip;

(7) Body feathers, especially on breast, with highly developed flexules on both distal and proximal barbules;

(8) Down barbules of moderate length, either with rather long prongs, longer near base of barbule (*Diomedea* and *Puffinus*), or with an even series of moderately developed prongs (*Oceanodroma* and *Pelecanoides*).

4. Order CICONIIFORMES

Under this large group are included four suborders, and as all the members of the group have little in common as regards their feather structure, it will be more convenient to deal with each suborder separately. The suborders are as follows: (1) Steganopodes, including all the water birds with fully webbed feet; (2) Ardeae, including herons and bitterns; (3) Ciconiae, the storks and ibises; and (4) Phoenicopteri, or flamingoes.

I. Suborder STEGANOPODES

Plates 18, 19

This suborder contains a rather heterogeneous assemblage of water birds, which, although probably all with the possible exception of the Phaëthontidae more closely related to each other than to any other birds and therefore forming a natural group, are very diverse, different members of it being probably near the line of descent of various more specialized groups. In all of them the plumules are evenly distributed over the entire body, and the after-shaft is absent in most genera, but a minute one is present in *Fregata*.

a) *Phalacrocorax penicillatus*

(1) *Remex*

Remiges highly developed but not as much so as in *Diomedea*. Shaft considerably broader than deep except at superior umbilicus, with narrow ventral groove often nearly obsolete; no fine striations on side of shaft as continuations of attachments of barbs, as there are in most birds. Barbs set about 20 per centimeter, almost equal on both vanes, very narrow, with only slight, translucent ventral ridge.

Inner vane.—About 40 barbules per millimeter on distal vanule,

20 on proximal, the proximal barbules being set at a much more acute angle with rami than are distals. *Distal barbules* (pl. 18, fig. 14a) moderate in size, the base being about 0.23 mm. long, pennulum about 0.45 mm. Base narrowed only slightly proximal to ventral teeth, and twist between base and pennulum not producing sharp curve in dorsal contour. Ventral teeth lobate in form, rather angular, and not smoothly rounded. Hooklets usually 5 in number, relatively short, but progressively becoming longer, their broadened middle portion drawn out and flattened, often with a tendency to give off a short prong. Ventral cilia long, curved, and not very flexible. Proximal 2 or 3 dorsal cilia broad and lobate, rather angular in shape, these followed by a few slenderer, spiny ones, the more distal ones more and more rudimentary. *Proximal barbules* (pl. 18, fig. 14b) with long, slender base about 0.6 mm. by 0.04 mm. Ventral teeth 4 or 5 in number, long and pointed, but not drawn out into wavy filaments as in *Procellariiformes*; pennulum slender and filamentous, slightly shorter than base.

Outer vane.—*Distal barbules* (pl. 18, fig. 14c) differ from those of inner vane in ordinary ways; shorter base, more numerous hooklets, and more proximal dorsal cilia undeveloped. Proximal barbules (pl. 18, fig. 14d) on basal portion of barbs resemble those of inner vane, but on distal half, more or less, ventral teeth separate from one another, increasing in number, and develop into hooked barbicels, which are shorter and have stouter hooks than those of the *Procellariiformes* (compare plate 18, figure 14d with plate 17, figure 10d).

(2) Other Feathers

In *upper back feathers* of females and young, distal barbules nearer type of outer vane of remiges, with narrow elongate base, two small, lobate ventral teeth, a long, broad pennulum with a double series of cilia, dorsal ones best developed towards tip, but never as well developed as the long, filamentous ventral ones. Pennula of barbules near middle of barbs longest, giving brown velvety effect to plumage (pl. 18, fig. 14e). Black edgings of feathers due both to imperfections of development and to subsequent wearing away of long pennula of distal barbules. Proximals with slender tapering base, about 0.4 mm. long, and much elongated slender pennula, about 0.8 mm. in length, with weak hooked cilia at bend, followed by some scattered, simple, filamentous ones (pl. 18, fig. 14f). Near base of barbs both proximal and distal barbules closely resemble those of remiges.

Dark glossy green feathers of adult male have elongated, weak barbules near base of barbs, the distals with an even series of short, hooked ventral cilia, reminiscent of penguins and loons. Glossy green portion produced by simple, rodlike barbules, slightly flattened, and with refractory surface.

Breast feathers have outer part of barbs furnished with weak, reduced barbules, entirely non-coherent, basal portion being well developed; distal barbules with long, narrow base, reduced ventral teeth, trapezoidal in shape, and elongate pennula, the latter with 3 or 4 short hooklets, and a complete series of short, curved, ventral

cilia, subequal in size. On more distal portion of barbs, sharp distinction between base and pennulum is lost, the barbules becoming very narrow and simple, with a few weak, curved ventral cilia near tip. Proximal barbules very much like those of back, but more simple, and on terminal portion of barbs assuming a form very similar to distals opposite them, except that the ventral barbicels are longer and more numerous.

b) Other Types

(1) *Plotinae*

Plotus, although grouped with the *Phalacocoracidae*, constituting the subfamily *Plotinae*, differs from *Phalacocorax* so widely in its feather structure that on this basis alone it should be entitled to full family rank. The *Steganopodes* as a group are characterized by the unusual difference in the different families as regards their minute feather structure, but no two families of the order are more distinct from each other than is *Plotus* from *Phalacocorax*.

Taking *Plotus anHINGA* as a type, we find that the distal barbules of the inner vanes of the remiges (pl. 18, fig. 13a) are remarkably reminiscent of those of the *Cathartidae*. The bases are elongate and narrow, about 0.35 by 0.03 mm., while the pennula are about 0.45 mm. long. The twist between the base and pennulum is of such a nature as to give the dorsal contour a peculiar, characteristic wavy curve. When spread back between thumb and forefinger both the base and the tip of the pennulum lie in a vertical plane, only the moderately broad hooklet area lying on its side, giving it a hump-backed appearance. The ventral teeth are lobate, and project straight forward in a direct line with the ventral edge of the base. The hooklets, usually five in number, are relatively short and stout, but progressively increasing in length; the ventral cilia are coarse, straight, and blunt, all but the proximal one or two being closely appressed to the barbules. All of the dorsal barbules are absent entirely, except the specialized one or two basal ones, which have the form of stout, blunt, forward and laterally projecting spines. Immediately distal to them the dorsal contour of the barbule curves evenly downward. The proximal barbules (pl. 18, fig. 13b) are hardly less peculiar. In these the base is short and stout, hardly longer than the base of the distals, and about 0.55 wide, with very short, triangular ventral teeth. The pennulum is remarkably short and stout, being considerably shorter than the abbreviated base, and 0.02 mm. wide, the cells of the ventral tooth region and beyond having conspicuous, recurved dorsal spines, and

all of the cells clearly marked off by ridges. The barbules are set fairly close together, the distals being about 30 and the proximals 18 per millimeter.

In the outer vane of the secondaries are to be found the most unusual types of barbules in the whole avian class. The portion of the vane which possesses a beautiful silvery grey color owes this entirely to the pennula of the distal barbules (pl. 18, fig. 13c). The bases are similar to those of the inner vane, but the pennula are profoundly transformed into thick, clumsy, inflated, sacklike expansions, filled with opaque air bubbles which, when the barbules are immersed in balsam, become infiltrated and rendered transparent, leaving the round nuclei appearing like eyelike spots. There are no dorsal cilia whatever, the hooklets are only three or four in number, short and heavy, and the ventral cilia are produced into extremely long, filamentous processes, lying closely appressed to each other, and extending far beyond the tip of the expanded portion of the pennulum. There are nine or ten short cells in the pennulum beyond the hooklet region, each with a long ventral barbicel, so that there is a dense brush of these. The deep black pigment of these barbules has a peculiar distribution, being dense in the base and in the hooklet cells and first two cilia cells of the pennulum, but absent in the terminal part of the pennulum. Distal to the silvery area, the pennula lose their inflated form and long cilia, then resembling those of the inner vane, but with no dorsal spinelike cilia. The proximals of the outer vane (pl. 18, fig. 13d) are hardly distinguishable from those of the inner vane, except that the pennulum is slightly shorter, and the recurved dorsal spines more prominent.

The back feathers of *Plotus* are modifications of the same type. The proximals (pl. 18, fig. 13g) have a similar short, relatively broad base, and the pennulum with recurved spines, but it is produced into a long, slender filament, and ultimately the whole barbule is transformed into down on the more basal barbs. On the more distal barbs the pennula become elongated and lose their broad character, at the same time developing a few very weak and minute ventral cilia, but the typical form of the whole barbule is then soon lost and it becomes merely rodlike in form with a few ventral barbicels. The distal barbules also ultimately assume this form at the tip of the barbs. On the black portion of the feather the distal barbules (pl. 18, fig. 13f) have long, slender bases with small but typical ventral teeth, no hump on dorsal contour between

base and pennulum, four very short, stout hooklets, and a tapering pennulum with a typical series of ventral cilia, but no dorsal ones. On the silvery grey portion the barbules resemble those of the similar portion of the secondaries, but are still more transformed. The base is shortened and greatly reduced, and the pennulum is enormously expanded and inflated (pl. 18, fig. 13e), with short reduced hooklets, and greatly elongated filamentous ventral cilia lying in a close, dense brush. The barbules of the back feathers are exceedingly dense, the distals being set 45 per millimeter, and the proximals only about 18 per millimeter.

The breast feathers of *Plotus anHINGA* are entirely downy, the barbules being short on the terminal portion of the feather, but long on the basal portion, where they are also very dense, there being over 50 per millimeter on each side.

(2) *Fregatidae*

The *Fregatidae*, containing only the genus *Fregata*, have the barbules of the remiges strikingly similar to those of *Phalacrocorax*, but differ in being of enormous size relative to the size of the feathers (pl. 18, figs. 15a, 15b). Comparing these figures with figures 14a and 14b of the same plate, which represent barbules of a feather of similar size in *Phalacrocorax*, the difference is plainly evident. The proximal barbules of the inner vane have a base which is 0.9 mm. in length. In spite of their large size they are set very close together, there being about 32 distals and 17 proximals per millimeter.

The iridescent feathers of the back have the barbules completely transformed for the production of color. The distal barbules of the iridescent purplish and greenish-black feathers have short, inconspicuous bases, three or four small moderate hooklets, and flat, expanded pennula with constrictions between the cells. This method of iridescent color production is exactly similar to that of ducks, and the pennula are of precisely the same type as that in *Anas platyrhynchos* (pl. 21, fig. 28i). In *Fregata* the proximal barbules also share in the iridescent effect by means of the prominent dorsal ridges between the cells bearing the ventral teeth, a condition frequently found in birds with dark iridescent feathers, e. g., *Geococcyx* (pl. 30, fig. 73a). These proximal barbules of *Fregata* have rather slender, tapering bases, and the ventral teeth tend to become separated, to increase in number, and to develop as short

stout, ventral barbicels. The pennula of the proximals are filamentous and take no part in the color production.

In the breast of *Fregata* the barbules are slender and elongated, with all the barbicels small and weak, but with no specialized characters.

(3) *Sulidae*

The Sulidae, containing the genus *Sula*, or gannets, are almost identical with the cormorants and frigate birds in the minute structure of the remiges, except in the smaller size of the barbules, and the slightly longer ventral teeth of the proximals of the inner vane (pl. 19, figs. 16a, 16b), and the better developed series of ventral barbicels of those of the outer vane, those representing the ventral teeth being short, broad, and blunt, followed by a series of perfectly formed, hooked cilia, broad at their origin, and tapering with the curve, as in the proximals of the outer vane of *Aechmophorus* (pl. 16, fig. 9d).

The back and breast feathers have barbules very similar to the less specialized ones of *Phalacrocorax* and *Fregata*. The distals (pl. 19, fig. 16c) are elongate, with short, stout hooklets and a full series of curved ventral cilia, the dorsal ones being less conspicuous. The proximals (pl. 19, fig. 16d) are also long and slender with a series of weak ventral cilia. Towards the tips of the barbs flexules are developed very much as in *Phaëthon*. (See below, and plate 19, figures 19e and 19f).

(4) *Pelecanidae*

The pelicans, Pelecanidae, with the single genus *Pelecanus*, while possessing the same essential characters of the barbules as do the cormorants, frigate birds, and gannets, differ in a number of details. In the remiges of *Pelecanus erythrorhynchus* the distal barbules of the inner vane (pl. 19, fig. 17a) are conspicuously short and stout. The base is over 0.06 mm. wide, and only about 0.25 mm. long, whereas if it had the same relative length as in *Phalacrocorax* it would be about 0.37 mm. long. The ventral teeth are very broad and lobate, the hooklets, about six in number, are relatively slender and progressively longer, followed by a series of long, slender ventral cilia, which lie close together on account of the shortness of the cells. The dorsal barbicels resemble those found in the more typical genera. In contrast to the distal barbicels, the proximals (pl. 19, fig. 17b) have exceedingly long and slender bases, being almost 0.9 mm. long and only about 0.06 mm. wide in the

middle portion of the barbs. The pennula are short, not over half the length of the bases. In no birds which I have examined is there a greater difference between the length of the bases of distal and proximal barbules on the same barb. To counterbalance this great difference in size, in order to produce fairly equivalent vanules, the angle of insertion of the distals is unusually wide, while that of the proximals is unusually acute, this in turn resulting in an astonishing difference in number of barbules per unit of measure. While there are 40 or more distals per millimeter, there are only 16 or 17 proximals for the same distance.

On the outer vane the distal barbules differ from those of the inner vane only in the absence of the dorsal cilia, and sometimes in the presence of one more hooklet. The proximals (pl. 19, fig. 17c), except on a small portion of the tip of the barb, are similar to those of the inner vane except that they are short, and relatively broader. On the distal part of the barb the ventral teeth increase to about six in number, become separated, and are transformed into very long, stout, curved barbicels, resembling the teeth of a large-toothed comb. The pennulum is shortened so that it does not extend more than one cell beyond the barbicels; the base is likewise shortened and reduced.

The primaries of *Pelecanus californicus* are similar to those described above. The secondaries and coverts, however, have the distals transformed to produce the characteristic hoary effect. These barbules (pl. 19, fig. 18a) have their bases reduced in size, the hooklets shortened, and the pennula elongated, with a double series of long, slender cilia. They resemble very closely the distal barbules of the hoary feathers of *Phalacrocorax* (pl. 18, fig. 14e), but the pennula are not so broad, while the cilia are longer and more prominent.

In the breast feathers of *Pelecanus*, at the base of the barbs the barbules have a structure similar to that found in *Sula* and other Steganopodes, a proximal barbule from this portion being shown in plate 19, figure 17e. The outer portion of the barb, however, develops typical flexules on both distal and proximal barbules, exactly as in the Procellariiformes. Plate 19, figure 17d, shows a distal barbule from a breast feather of *P. erythrorhynchus* and comparison with plate 17, figure 10e (*Diomedea exulans*) will show the striking similarity. At the extreme tip both barbules assume the form shown in plate 19, figure 19e (*Phaëthon*), which

should be compared with plate 17, figures 12a and 12b. *Pelecanus californicus* has the same type of structure.

(5) *Phaëthontidae*

The Phaëthontidae or tropic birds, as far as feather structure is concerned, seem to show a perfect transition from the Procellariiformes on the one hand to the Laro-limicolae on the other, though apparently more closely related to the latter. As shown by plate 19, figure 19a (*Phaëthon rubricauda*), the base of the distal barbules of the inner vane is relatively large and broad, and the ventral teeth long and slender, with a very slight tendency to bifurcate, not always displayed, however. The hooklets are only four in number, and relatively short and small, the ventral cilia are much reduced, and the dorsal ones likewise, except the basal two, which are strongly reminiscent of Laro-limicolae. The proximal barbules (pl. 19, fig. 19b) differ from those of other Steganopodes, but agree with the Laro-limicolae in their relatively small size, and in having small inconspicuous ventral teeth. There is another significant difference in the relative number of distal and proximal barbules. In all other Steganopodes there are nearly twice as many distals as proximals, while in *Phaëthon* there are 22 or 23 proximals to 30 distals, this genus thus resembling both the Procellariiformes and the Laro-limicolae. The barbules of the outer vane, the forms of which are shown in plate 19, figures 19c and 19d, are characterized primarily by their slender form, the wide separation of the hooklets of the distal barbules, which are all of nearly equal length, and the weak ventral cilia of the proximal barbules. The rami of the outer vane have the ventral edge serrate and broken into villi, a condition which reaches the height of its development in the Anseres.

The barbules in back feathers of *Phaëthon rubricauda* closely resemble those of the inner vane of the remiges, except in their smaller size.

The breast feathers, as in *Pelecanus* among Steganopodes, and like the Procellariiformes and Laro-limicolae, develop flexules, but not as numerous or as well-formed ones as in *Pelecanus*. Plate 19, figure 19e, shows a proximal barbule from the terminal portion of a barb from a breast feather, while figure 19f of the same plate shows a distal barbule from a portion not quite so near the tip. Its base is much reduced, and it has weak barbicels; a little more distally it assumes a form similar to that represented in plate

19, figure 19e. Unfortunately these two figures were reversed in position from the system usually followed in the preparation of the plates.

c) Down

The down of Steganopodes, like the pennaceous structure, is extremely variable. In *Phalacrocorax*, *Fregata*, *Pelecanus* and *Phaethon* the downy barbules are of moderate length, i. e., from 1.0 to 1.3 mm., and smoothly filamentous except in *Pelecanus*, which has minute prongs at the nodes on the distal portion of the barbules. In *Plotus* the downy barbules (pl. 34, fig. 99) are also filamentous, but are very long, frequently reaching a length of over 2 mm. *Sula* differs not only from other Steganopodes but also from all other birds in the enormous development of the prongs at the nodes. These reach a length of over 0.1 mm. in barbules which are only 0.6 to 0.8 mm. long, being slender, filamentous, and frequently bifurcated (pl. 34, fig. 98). The only other birds which begin to approach *Sula* in the length of the prongs are albatrosses and puffins, and this might be looked upon as additional evidence of fairly close relationship between the Sulidae and the Procellariiformes.

d) Relationships

The Steganopodes are a group of birds in which primitive characters are curiously combined with specialized characters, the result being a rather heterogeneous aggregation of more or less related forms which are specialized along different lines. They seem to fall into three fairly well-defined groups as follows: (1) *Phalacrocorax*, *Fregata*, *Sula* and *Pelecanus*; (2) *Plotus*; and (3) *Phaethon*.

The first group may be regarded as containing the most typical Steganopodes, since they form the bulk of the group, and are least specialized. They seem undoubtedly to be derived from a primitive procellariiform type, and as certainly to stand at the base of the ciconiiform group, the next above them being the Ciconiinae.

The second group, including only the neotropical genus *Plotus*, though often grouped only as a sub-family of the Phalacrocoracidae, differs very widely from the other Steganopodes in the structure of its feathers, in which it is very specialized. In some details of the feather morphology this genus shows such striking similarity

to the Cathartae that their kinship can hardly be doubted. This will be forcibly shown by a comparison of plate 18, figures 13a and 13b, with plate 22, figures 34 a and c. This close similarity of the Cathartae with *Plotus*, accompanied as it is by other common characters as shown by Gadow (1891), suggests the possibility of regarding the Cathartae as direct descendants of the Steganopodes, from a form not far removed from *Plotus*.

The third group, Phaëthontidae, is so strikingly like the Laridae that their affiliation with the Steganopodes seems very doubtful, and if feather morphology be considered, they should be looked upon rather as aberrant larid forms. Comparison of plate 19, figures 19 a-f, with plate 28, figures 61 a-e, will make clear the marked similarity in feather morphology.

e) Summary

The Steganopodes are divisible into three groups on the basis of feather morphology, the typical Steganopodes, *Plotus*, and *Phaëthon*. The first group is characterized as follows:

- (1) Plumules uniformly distributed;
- (2) Aftershaft absent or rudimentary;
- (3) Distal barbules of remiges relatively small as compared with proximals, and much more numerous, the difference in numbers much greater than usual;
- (4) Distal barbules of remiges with short, broad base, with broad lobate ventral teeth, except in *Sula*, where they are relatively small and narrow; pennulum moderate in length, hooklets slender and progressively longer, ventral cilia long and slender, basal dorsal cilia, on inner vane, stout and triangular, gradually changing to a spiny, and ultimately a filamentous form;
- (5) Proximal barbules of remiges with base long and large relative to distals; ventral teeth long and conspicuous on inner vane, transformed into a weak series of ventral cilia on outer vane; pennulum rather broad, usually shorter than base, but sometimes as long.
- (6) Back feathers with bases of both distal and proximal barbules elongate, the distals with long pennula, with double series of well-developed slender cilia, except where specially modified for production of iridescent color; hooklets short; proximal barbules with tendency to develop weak ventral cilia;

(7) Breast feathers similar but weaker, without flexules except on outer part of barbs in *Pelecanus* and *Sula*;

(8) Down barbules of moderate length, smoothly filamentous, or with minute prongs at nodes on their distal portion except in *Sula*, where prongs at nodes are enormously developed, to an extent approached among other birds only in some Procellariiformes.

Plotus, constituting the second group, is characterized as follows:

(1) Proximal barbules very small relative to distals, the length of their bases actually less.

(2) Distal barbules of inner vane of remiges with ventral teeth lobate, their ventral edge in a continuous line with ventral edge of base; hooklets relatively small and very stout, progressively longer; ventral cilia coarse, blunt, and rodlike, more or less appressed to pennulum; no dorsal cilia except one, or sometimes two, stout, blunt, spinelike basal ones, followed by a dip in the dorsal contour of the barbule, thus giving it a characteristic shape.

(3) Proximals of both vanes of remiges with very short, small base, inconspicuous ventral teeth, and short, conspicuously wide pennulum, with recurved spines.

(4) Silvery gray color of parts of outer vane due to a greatly expanded and inflated unpigmented pennulum bearing small, stout hooklets and extremely long, slender, closely associated ventral cilia.

(5) Body feathers with distals and proximals both similar to remex type, of which they are mere simplifications; no flexules developed.

(6) Down barbules smooth and filamentous, and longer than in any other Steganopodes, frequently over 2 mm.

The third group, including only the monogeneric *Phaëthontidae*, is characterized as follows:

(1) Distal barbules of remiges large as compared with proximals, and the latter over two-thirds as numerous.

(2) Twist between base and pennulum of distals producing sharp curve in the dorsal contour as barbule lies in normal position; ventral teeth small and slender; hooklets slender, rather weak, and well separated from each other; ventral cilia reduced; and basal dorsal cilia of inner vane lobate, almost exactly as in gulls.

(3) Proximal barbules of remiges with narrow base, short pennulum and short inconspicuous ventral teeth on inner vane, a series of weak ventral cilia on outer vane.

(4) Breast feathers with flexules developed on terminal portion of barbs of breast feathers.

(5) Down smooth and filamentous, little if any over 1 mm. long.

II. Suborder CICONIAE

Pl. 20, Figs. 23-27

Constituting the second suborder of the Ciconiiformes are the storks and ibises, which, together with the Ardeae, form a compact and well-defined group. Although the typical Ardeae are readily distinguishable from typical Ciconiae, there are a number of more or less intermediate forms which make their characterization by other characters as well as by epiphylogeny very difficult. Excluding *Balaeniceps* and *Scopus*, which combine characters of both groups, the Ciconiae are distinguished from the Ardeae by the following characteristics: (1) absence of powder down, (2) even distribution of plumules in both pterylae and apteria, and (3) feathered lores. The aftershaft is very variable, being present, rudimentary, or absent in different genera.

a) *Mycteria americana*

(1) *Remex*

Shaft stout and square, about as deep as wide, with broad, V-shaped ventral groove, and fine striations on sides where barbules are attached. *Rami* not greatly deepened at junction with shaft but deeper than usual in Steganopodes. Pith cells more than a single layer thick, and ventral edge of rami of both outer and inner vanes without villi. *Distal vanule* with barbules greatly outnumbering those of *proximal vanule*, the barbules about 40 per millimeter on former, only 18 per millimeter on latter, this difference accompanied by great difference of angle of insertion of barbules on ramus.

Inner vane.—*Distal barbules* (pl. 20, fig. 23a) small relative to proximals; base of moderate size, about 0.35 by 0.05 mm., with fairly large, lobate ventral teeth, frequently blunt and slightly incised at tip; pennulum characterized by stout heavy form; hooklets numerous, 6 or 7 in number, moderately stout, and progressively increasing a great deal in length; ventral cilia rather poorly developed, present all the way to tip of pennulum, straight, and appressed to barbule; basal dorsal cilia stout, blunt, and spine-like, well separated from each other, the first one always the largest; usually three such stout barbicels developed, the following ones becoming more and more like the ventral ones. *Proximal barbules* (pl. 20, fig. 23b) with very large bases, about 0.7 mm. long by 0.07 mm. wide with a series of broad, triangular ventral teeth projecting very little beyond the ventral contour of barbule; pennulum re-

markably short, about half length of base, very broad proximally, and tapering rapidly to tip; pigment deeper ventral to nuclei than dorsal to them, reverse being more frequently true in other birds.

Outer vane.—*Distal barbules* differ only in absence of dorsal cilia, except a few terminal rudimentary ones (pl. 20, fig. 23c). *Proximals*, unlike those of any birds so far studied except pelicans, differ only slightly from those of inner vane, being somewhat smaller, their form exactly similar except that ventral teeth are slightly longer, with tendency to become hooklike, but even at tip of barbs not increasing in numbers and forming a series of ventral barbicels.

(2) Other Feathers

Back feathers have same structure as outer vane of remiges except that small dorsal cilia are sometimes developed on distal barbules near the base of more proximal barbs. In *breast feathers* structure not essentially different. Distals (pl. 20, fig. 23d) more elongate, and dorsal cilia, except at proximal end of pennulum, better developed. Proximal barbules of exactly same type as in remiges, in neither distal nor proximal barbules any tendency whatever for development of flexules.

b) Other Types

Ciconia ciconia has a very similar structure of its feathers. The chief difference is in the relative narrowness of the proximal barbules.

Leptoptilus dubius has a slight modification of the structure of distal barbules as compared with those of *Mycteria*. The first two dorsal barbicels of distal barbules of the inner vane (pl. 20, fig. 24a) are stout and spinelike as usual, but are very much closer together and are not followed by a series of less specialized cilia, thus approaching more closely to the heron type. On the outer vane the pennulum of distal barbules is relatively short and furnished with an even series of short blunt dorsal cilia (pl. 20, fig. 24b). The under tail coverts of *Leptoptilus* deserve special mention as they are the source of the famous "marabou" feathers of commerce. These feathers are furnished with stiff, heavy shafts, but have the entire feather downy in structure, a condition seldom found in contour feathers, except occasionally on a very weakly developed breast or belly feather.

In *Plegadis guarauna*, or scarlet ibis, there is a very striking modification in the distal barbules to deepen the scarlet color-effect (pl. 20, fig. 26a). As will be seen from this figure, both base and pennulum are profoundly transformed, and all the barbicels except the hooklets are lost or greatly changed. Both base and pennulum

are characterized by a series of transverse rings which evidently have a tendency to break up the light and deepen the red color produced by the diffused pigment. The proximal barbules remain practically unchanged.

Ajaja ajaja, representing the Plataleidae or spoonbills, resembles *Plegadis* very closely. Both *Plegadis* and *Ajaja* have the ventral edge of the rami serrate. The similarity of the barbules of the back feathers to similar ones of *Mycteria* is shown by plate 20, figure 27a, as compared with plate 20, figure 23c.

c) Down

The down barbules of *Mycteria americana* and of other Ciconiidae are long, frequently over 2.5 mm., and are very slender and filamentous, with minute inconspicuous prongs, or none whatever, at the nodes. In the Ibisidae and Plataleidae, on the other hand, the down barbules are rather short, usually under 1 mm. in length, and very stout and coarse, the internodes with longitudinal ridges and grooves, and the nodes with well-developed prongs. A down barbule of *Guara rubra* is shown on plate 23, figure 101.

d) Relationships

The Ciconiae form the middle section of the Ciconiiformes, the Steganopodes being below them and the Ardeae and Phoenicopteri above. Undoubtedly their closest relatives are the herons, with which they are joined by such intermediate forms as *Balaeniceps* and *Scopus*, the feathers of which I have been unable to obtain for study. The Phoenicopteri appear to connect the Ciconiae with the Anseres. No relation whatever is shown by the structure of the feathers to the Limicolae or to typical Gruiformes.

e) Summary

The Ciconiae are characterized as follows:

(1) Barbules much more numerous on distal than on proximal vanule.

2. Distal barbules with base of moderate size relative to proximals, with moderate, lobate ventral teeth; pennulum stout and heavy, with 6 or 7 moderate-sized, progressively longer hooklets; ventral cilia more or less appressed, straight, usually blunt; on the inner vane about three well-separated, stout, basal dorsal cilia, followed by less

specialized ones, except in *Leptoptilus*, where there are only 2, and these close together.

(3) Proximal barbules with large bases, inconspicuous ventral teeth, a short but broad and tapering pennulum, and no ventral cilia developed on outer vane.

(4) Ventral edge of outer rami of primaries serrate in Ibididae and Plataleidae, but smooth in Ciconiidae.

(5) Body feathers with barbules as in remiges, but more elongate and slender; never any flexules.

(6) Down barbules in Ciconiidae long, slender, and filamentous, with small inconspicuous prongs or none at all; in Ibididae short, stout and heavy, longitudinally ribbed, and with well-developed prongs at the nodes.

III. Suborder ARDEAE

Pl. 20, Figs. 20-22

As stated above, the typical Ardeae are readily distinguishable from the Ciconiae, but *Balaeniceps* and *Scopus* combine the characters of both groups in such a way that the characterization of either is very difficult without allowing for these exceptions. Unfortunately I have not been able to obtain feathers of either of these genera for study, in order to find out whether their feather structure adheres to the typical ardean type or approaches that of the Ciconiae. Having no data concerning either of these two outlying forms, nor of *Cochlearius*, the present section deals only with the Ardeidae, including the herons, egrets and bitterns. Their general epiphylogenetic characteristics are as follows: (1) plumules confined to the apteria, (2) powder down present, (3) aftershaft present, and (4) lores naked.

a) *Ardea herodias*

(1) *Remex*

Shaft and *rami* very similar to those of Ciconiae, the shaft, if anything, slightly deeper than wide, with V-shaped ventral groove, and fine striations on side. Rami not considerably deepened, even on outer vane, the pith not more than a single layer in thickness and the ventral edge not serrate or furnished with villi. Distal vanule with about 30 barbules per millimeter, proximal vanule with about 18 per millimeter.

Inner vane.—*Distal barbules* (pl. 20, fig. 20a) with small base, about 0.26 by 0.04 mm. with relatively very large, leaf-like ventral teeth so shaped and arranged as to form a single, large, blunt,

subtriangular lobe; pennulum with very characteristic form, differing considerably from those of Ciconiae, though approached in *Leptoptilus*; hooklets similar to those of Ciconiae, but normally only 5 in number, followed by 3 or 4 steadily diminishing ventral cilia, beyond which the pennulum is greatly elongated, rather slender, and totally unbarbicelled; 2 basal dorsal cilia developed as characteristic stout spines very closely approximated to each other, third dorsal cilium a short spine, and all the rest undeveloped. *Proximal barbules* (pl. 20, fig. 20b) with base of moderate size, about 0.5 by 0.05 mm., with short, inconspicuous ventral teeth; pennulum only a little shorter than base, slightly flattened proximally, but soon tapering to a very fine slender filamentous tip.

Outer vane.—*Distal barbules* (pl. 20, fig. 20c) with pennulum somewhat shorter and stouter than in inner vane, usually 6 hooklets, no dorsal cilia, and a large number of short, blunt ventral cilia. *Proximal barbules* (pl. 20, fig. 20d) differ from those of inner vane only in having a somewhat shorter pennulum; no ventral cilia ever developed.

(2) Other Feathers

Inner scapular feathers with distal barbules (pl. 20, fig. 20e) somewhat like those of distals of outer vane of remiges, but both base and pennulum more elongated, pennulum also stouter, more like ciconiid type, with short, broad, and very blunt ventral cilia somewhat resembling ventral teeth; pigment irregularly distributed, being dense in base, but very light or absent in pennulum. *Proximal barbules* of scapulars (pl. 20, fig. 20f) differ from those of outer vane of remiges only in more elongate and relatively slender form. Blunt ventral cilia of distals of outer vane slightly more numerous and better developed, otherwise vanes alike. Elongated tips of these feathers produced by an elongation of the slender shaft accompanied by a number of greatly elongated barbs lying so closely appressed, and attached to shaft at such long intervals, as to lie parallel with shaft. These elongated barbs are furnished with distal and proximal barbules only slightly reduced, so that they interlock fairly well. On account of change in angle of insertion of more distal barbs, there is too much strain for perfect vane to be maintained, result being a breaking up into elongated groups of barbs, which is very characteristic of these feathers.

On *breast feathers* also with elongated, ornamental tips, basal portion of feathers has much simplified barbules, and barbs very loose if at all held together. Barbs of ornamental tip better developed with less simplified barbules, the latter resembling those of scapular and back feathers, being short, with well-developed functional hooklets. As in back feathers, barbs inserted at wide intervals, and closely appressed to one another so as to form a very narrow, compact tip.

b) Other Types

Nycticorax nycticorax differs from *Ardea herodias* in the structure of its remiges only in the slightly better developed third dorsal

cilium, and presence of a rudimentary fourth one. The dark green feathers of the back are somewhat modified. The bases of both distal and proximal barbules of these feathers are long and narrow, and deeply pigmented, while the ventral teeth in both are poorly formed and lightly pigmented. The hooklets of the distals are weak and reduced, the ventral cilia are short and blunt, and there are no dorsal cilia. The proximals have three or four progressively diminishing blunt ventral cilia on the pennulum, thus greatly resembling in general form the distal barbules.

Botaurus and *Butorides* very closely resemble *Ardea* in all the details of their feather structure. The distal and proximal barbules of the outer vane of *Butorides virescens* are shown in plate 20, figures 21a and 21b, and comparison with figures 20a and 20b of the same plate will show the similarity. The slight separation and forward curve of the ventral teeth of the proximals of the distal part of the outer vane, as shown in plate 20, figure 21b and slightly less prominently in plate 20, figure 20d, are very characteristic of the entire family.

The most interesting birds of the entire group from a popular point of view are the egrets, *Egretta candidissima* and *Herodias egretta*, from which are derived the famous "aigrettes" of commerce. In the structure of its remiges *Herodias egretta* differs from the typical forms of the genus *Ardea* in the reduction of the dorsal cilia. The first one is fairly well developed, the second smaller, and the third very minute. They thus differ from *Ardea herodias* in the opposite direction from *Nycticorax*, which has the dorsal cilia a little better developed.

The aigrettes of both species of egrets are too well-known to need a general description, the barbs being very widely separated on the shaft, reaching a length of 15 cm. or more, and appearing as filamentous strands entirely separate from each other. Although to the naked eye the barbs appear destitute of barbules, closer examination shows that there is a complete series of closely appressed, non-interlocking barbules, the distal and proximal ones very similar, except that the latter are a little longer. They are flat and tapering, with no well-developed barbicels, as shown in plate 20, figure 22. The distal and proximal barbules are spaced 21 and 18 per millimeter respectively. The barbules of the aigrettes of *Herodias egretta* differ from those of *Egretta candidissima* in the length, the former being under 0.65 mm. long while the latter are normally at least 0.7

mm. and usually a little over 0.8 mm. In the egret-like feathers of *Bubuleus ibis* of Europe there are only 11 proximal barbules and 14 distals per millimeter, and they never exceed about 0.57 mm. in length. These barbicels are even more rudimentary than in the true American egrets.

Eurypyga (see p. 352, and pl. 27, figs. 55a-d) and possibly *Cariama* (p. 352, and pl. 27, figs. 56a and b) are probably nearly related to the Ardeae. *Cursorius*, family Glareolidae (p. 356, and pl. 28, figs. 60a-c), also appears to be most nearly related to the Ardeae.

c) Down

The down barbules in *Ardea* are long, reaching a length of 2 mm. or more, being filamentous and very slender, with slightly enlarged nodes, and pigment uniformly, or almost uniformly, distributed. Minute prongs present at nodes on more distal portion of barbules. In *Botaurus*, in which the down is dark gray, the pigment is absent only at the nodes (pl. 34, fig. 100).

d) Relationships

The Ardeae, or at least the Ardeidae, seem to form an end branch from a ciconiid stem, being considerably more specialized than the Ciconiae, and apparently not giving rise to any other orders or suborders. *Eurypyga*, and to a less extent, *Cariama*, both ordinarily classed in the Gruiformes, have a feather structure which is so heron-like that the possibility of their inclusion in the Ardeae is strongly suggested. *Cursorius* likewise has a structure which strongly argues for its inclusion in this group.

e) Summary

The typical Ardeae have the following epiphylogenetic characters:

- (1) Plumules confined to apteria.
- (2) Aftershaft present.
- (3) Powder down present.
- (4) Lores naked.
- (5) Distal barbules nearly twice as numerous as proximals.
- (6) Distal barbules of remiges with small base, with large, leaflike ventral-teeth, so shaped and arranged as to form a large blunt triangle; hooklets usually 5, only 3 or 4 progressively dimin-

ishing ventral cilia developed, and on inner vane two closely approximated, blunt, stout, dorsal cilia followed by one or two spinelike ones, the rest of the pennulum elongated, slender, and without barbicels.

(7) Proximal barbules of inner vane with moderately large base, short inconspicuous ventral teeth, and pennulum very slender and threadlike, shorter than base.

(8) Proximals of outer vane similar to those of inner vane, never developing ventral cilia.

(9) Body feathers with pennulum of distals usually rather stout, dorsal cilia not developed, the ventral ones conspicuously short and blunt.

(10) Ornamental plumes with divided vanes frequently developed.

(11) Down very long, often over 2 mm., the nodes slightly enlarged, sometimes with minute prongs, pigment when present not collected into conspicuous spots.

IV. SUBORDER PHOENICOPTERI

Pl. 21, Fig. 32

The flamingoes, in Knowlton's classification, are grouped as a suborder of the Ciconiiformes, but in their characters they are so perfectly transitional between the Ciconiae, especially the ibises, on the one hand, and the Anseriformes on the other, that, while evidently forming a suborder of their own, the question as to the group with which they are more closely associated has been one of the most debated questions in the classification of birds. Their feather structure, therefore, is of unusual interest, on account of the light which it throws on this relationship.

As in both the Ciconiae and the Anseriformes, the down is here also uniformly distributed. The aftershaft is present, which is an interesting fact considering that in the Ciconiae it is very variable, while in the Anseriformes it is rudimentary or absent. There are twelve primaries as in some Ciconiae, whereas in Anseriformes there are only eleven.

a) *Phoenicopterus ruber*

(1) *Remex*

Shaft of remiges slightly wider than deep, with shallow median groove. Pith of *rami* more than one cell in thickness; whole ventral

ridge narrow, and without villi on the ventral edge on outer vane. Distal barbules small relative to the proximals, and outnumbering them about two to one; on inner vane of secondary about 40 distals to 20 proximal barbules per millimeter.

Inner vane.—*Distal barbules* (pl. 21, fig. 32a) with very short base, about 0.2 mm. long by about 0.04 mm. wide; ventral teeth slender and elongate, much more so than in *Ciconiae*, but less so than in *Anseres*; the pennulum relatively short, seldom over 0.3 mm., making, with the base, a short barbule; hooklets 5, slender, of moderate length, but progressively longer; ventral cilia long and slender, and not conspicuously curved; dorsal cilia, as a series, well developed, the basal 2 or 3, stout and spiny, the more distal ones more slender. *Proximal barbules* with base about 0.5 mm. long by 0.055 mm. wide, with a series of about 4 ventral teeth, the proximal two larger and more lobate, the outer ones more slender and pointed.

Outer vane.—*Distal barbules* differ mainly in the larger number of hooklets, and more conspicuous ventral cilia, and absence of dorsal ones, while in proximals (pl. 21, fig. 32b) the ventral teeth, especially distal ones, become separated from each other, increase in number, and form a series of straight, sharp, ventral barbicels, exactly comparable to those in the outer vane of ducks, as will be seen by comparing plate 21, figure 32b, with plate 21, figure 28f.

(2) Other Feathers.

In body feathers barbules merely a simplification of remex type, proximals retaining a series of slender, ventral barbicels, as shown in plate 21, figure 32c, which represents a proximal barbule from loose-vaned scapular feather; no flexules ever developed.

(3) Down

Down barbules (pl. 35, fig. 102) long and filamentous, with inconspicuous nodes except near tip of pennula, where they are slightly enlarged, and possess small prongs.

b) Relationships and Summary

In all of the above details of the minute structure of the feathers the *Phoenicopteri* agree with the *Anseres* more closely than with the *Ciconiae*.

In all of the following points they agree with the *Anseres* as opposed to the *Ciconiae*: (1) general shape and relative size of barbules; (2) form of ventral teeth of both distals and proximals; (3) form of both ventral and dorsal cilia of distals; (4) presence and form of ventral barbicels of outer proximals.

The chief points of difference are: (1) the smaller number of hooklets; (2) the smooth ventral edge of rami of outer vane; (3) form of down. In the first two* of these characters they also differ from the *Ibididae*, with which they are more closely related than

with any other Ciconiae, and in the third they are intermediate between the Ciconiae and the Anseres.

5. Order ANSERIFORMES

Pl. 21, Figs. 28-31

Comprising the two suborders Anseres and Palamedeae, this order is characterized by the uniform distribution of plumules, and the absence or rudimentary condition of the aftershaft. The Palamedeae are further characterized by the total absence of apteria, a condition found elsewhere only in the Sphenisciformes among carinate birds. Since in the finer structure of their feathers the two suborders have little in common, it will be more advantageous to take them up separately.

I. Suborder ANSERES

Pl. 21, Fig. 28-30

a) *Anas platyrhynchos*

(1) *Remea*

Calamus unusually long, being considerably over one-third length of quill in primaries. This elongation is a very constant and characteristic feature. *Shaft* about as broad as deep, with broad, shallow ventral groove. *Rami* with rather broad attachment to shaft, especially on outer vane, and differing from all other birds except a few gallinaceous species, in the enormous development of ventral ridge into a broad, thin, filmlike expansion on the basal one-third to two-thirds of the barb, reaching over and adhering to the adjacent ramus in front of it, producing a very conspicuous macroscopic effect on lower side of feather, where the portion of feather plate involved has a shiny, glazed appearance. Plate 21, figure 28a, represents proximal portion of barb from inner vane of a primary, showing expanded ventral edge with filmy expanded ventral ridge ending abruptly. On outer vane, rami further characterized by dense villi (pl. 21, fig. 28b). Distal and proximal *vanules* with barbules not as different in size as in Ciconiae but distals outnumbering proximals nearly as much as in latter group; about 42 distals and 23 proximals per millimeter on a barb from inner vane of primary.

Inner vane.—*Distal barbules* (pl. 21, fig. 28c) relatively large for size of feather, base about 0.27 by 0.042 mm., extremely thin and filmy, pigment usually absent below line of nuclei, although this area is wider than usual; ventral teeth lobate but not blunt or truncate at end, being drawn out more or less into slender points. Hooklets exceedingly slender and delicate, with their hooked tips somewhat enlarged, usually 6 or 7 of them, progressively and regularly becoming longer; ventral cilia long, slender, and not

appressed. Dorsal cilia forming a well-developed series, basal ones stouter and spinelike, but not as strongly contrasted with others as in Ciconiae. *Proximal barbules* (pl. 21, fig. 28d) also thin and filmlike, with little pigment; base unusually slender, about 0.65 by 0.04 mm. Proximal two ventral teeth broad, lobate, and blunt, followed by two or three narrow and pointed ones; pennulum little shorter than base, with rudimentary barbicels always showing.

Outer vane.—*Distal barbules* (pl. 21, fig. 28e) with drawn-out points of ventral teeth more prominent; hooklets even more slender, and increased in number; dorsal barbicels absent. *Proximal barbules* on outer portion of barb with ventral teeth proliferated and transformed into straight ventral barbicels, resembling teeth of a comb (pl. 21, fig. 28f).

(2) Other Feathers

As in nearly all ducks, greater wing coverts form a *speculum* of different color from rest of wing, in this case deep bluish violet. For production of this color, as of other metallic colors, e. g., blues and greens of various species, the pennula are transformed into flattened refrangent surfaces (pl. 21, fig. 28i) with constrictions between cells, and fine, longitudinal striations on cells, which are deeply pigmented with black. Base and hooklet region considerably reduced in these metamorphosed barbules. Barbules of inner vane of speculum feathers, and proximals of outer vane also, unmodified. As described at close of Part I (p. 279), modifications of distal barbules are absent in albinos.

Body feathers rather loose in texture, due largely to fact that bases of barbules lie in vertical plane, leaving wide spaces between them. Ventral teeth of distal barbules greatly reduced, but slender, subequal cilia still numerous and well formed. Just distal to hooklet region, pennulum twists so that ventral cilia come to project dorsally. Proximals have slender, tapering bases, inconspicuous ventral teeth and rudimentary prong-like cilia. The poorly developed *tail feathers* intermediate in form between remiges and body feathers. Their form is shown by plate 21, figures 28g and h.

b) Other Types

The minute structure of the feathers is remarkably constant in all the members of the Anseres. *Nettion carolinense* is perhaps slightly more typical of the group in that the ventral teeth of the distal barbules are greatly elongated and slender, as shown in plate 21, figure 29a. *Marila*, *Mergus*, *Querquedula* and other genera are almost identical with *Nettion*.

Branta, like *Anas*, has the ventral teeth of the distals somewhat shorter, while some of the feathers have the pennula of the distals of the outer vane elongated with long brushlike cilia to produce the characteristic plush-like effect. *Chen* very closely resembles *Branta*,

but the barbicels of the proximals of the outer vane are stouter and more irregular.

Olor columbianus has the elongation of the ventral teeth of the distals less extreme, as in *Anas*, and has the hooklets even more slender than in typical ducks and geese.

Speculum feathers occur in a very large number of genera, especially of ducks, sometimes being white, but frequently some iridescent color, as blue, green, or violet, the structure in these cases being of the type described above for *Anas platyrhynchos*. A distal barbule from the brilliant green portion of a speculum feather of *Nettion carolinense* is shown in plate 21, figure 29b. The deep velvety black scapular feathers of *Mareca*, which are tinged with metallic green, have distal barbules in which the base as well as the pennulum takes part in the color effect (pl. 21, fig. 30a).

c) Down

The down barbules of all typical ducks are short, seldom over 1 mm. long, and usually considerably less. They are simple and thread-like for the greater part of their length, but on the basal half of the barbs there are developed at the tip of the barbules 3 or 4, sometimes 5, very conspicuous expanded nodes followed by a slender tip (pl. 35, fig. 104). On the outer portion of the barbs these enlarged nodes are reduced and there are a few terminal pairs of prongs taking their place. The number of terminal nodes differs to some extent in different species, e. g., *Anas* has 2 or 3, *Mareca* 3 to 5, and *Mergus* 2 to 4. In *Branta* there are 4 to 6, which are not so large and are farther separated. In *Olor* they are still more separated, less conspicuous, and the transitional nodes on either side are better developed (pl. 35, fig. 103).

d) Relationships

The feathers of the *Anseres* show high specialization in a number of points of their microscopic morphology, and are unquestionably to be regarded as the end of one line of evolution. The typical ducks show the specialized characters in their highest development, the geese, as represented by *Branta* and *Chen*, being lower in the scale, and the swans, as represented by *Olor*, still lower and forming a more or less natural bridge over the gap between the more typical *Anseres* on the one hand, and the *Phoenicopteri* on the other.

•

e) Summary

The Anseres are characterized as follows:

- (1) Plumules evenly distributed.
- (2) Aftershaft rudimentary or absent.
- (3) Rami of remiges with extremely broad filmlike ventral ridges, furnished with dense villi on the ventral edge on the outer vane.
- (4) Barbules of remiges and body feathers essentially the same, the latter merely simplified.
- (5) Distal barbules with elongated ventral teeth and very slender hooklets.
- (6) Proximal barbules of inner vane with slender base, 2 proximal ventral teeth blunt and lobate, the others narrow and pointed, and a moderately long filamentous pennulum with pronglike rudimentary barbicels.
- (7) Proximals of outer vane with a series of straight, pointed cilia on the pennulum.
- (8) Down barbules short, with nodes undeveloped, except 3 to 6 or 8 near tip which are very highly developed.

Suborder PALAMEDEAE

Pl. 21, Fig. 31

The two genera constituting this group, *Palamedea* and *Chauna*, differ in a number of important details of feather structure from the Anseres. In *Chauna cristata* the barbs are heavily built, the pith more than one cell in thickness, and with only a narrow translucent ventral ridge. The distal barbules (pl. 21, fig. 31a) of the outer vane, the only ones which I have obtained for study, are characterized by a large, stout base with broad, lobate ventral teeth, reminiscent of the Meleagridae, and by a fairly short pennulum with a very large series of long slender hooklets, usually eight in number, followed by only a few slender ventral barbicels. The proximals (pl. 21, fig. 31b) have large, stout bases with the ventral teeth as in the Anseres (i. e., the first two more lobate than the others), and a short, rather broad pennulum as in the Ciconiae and also some Galli.

The back feathers are of a rather peculiar nature, the pennula being greatly elongated to give the characteristic hoary appearance. The base is long and tapering, the hooklets usually five, subequal in size, followed by a complete series of ventral cilia, also of approx-

imately equal size. The long barbicelled pennulum is without pigment, resulting in the hoary appearance above mentioned. The breast feathers have a much simplified type of barbules, with a series of hooklets and curved ventral cilia which grade into each other and are all subequal in size. The pigment is distributed in well-defined transverse bars. The down barbules, unlike those of the Anseres, are long, 2 mm. or more, being almost simple threads, a few inconspicuous prongs being developed at the nodes.

As will be seen from the above, the Palamedeae are peculiar in that they combine the characters of a number of other groups of birds in a confusing manner and could not readily be associated with any group on the basis of their feather structure. The distal barbules of the remiges resemble those of the Anseres in number and form of the pennular barbicels, but the ventral teeth are most closely paralleled by the Meleagridae; proximals of the remiges combine anserine, ciconiid, and galline characters; the barbules of the breast feathers constitute a type of their own, probably degenerated; and finally the down barbules are long and threadlike, unlike either Anseres or Galli, but near the Ciconiidae.

6. Order FALCONIFORMES

Plates 22, 23

The Falconiformes include a rather well-defined group divisible into three distinct suborders, which, as in the case of Anseriformes and Ciconiiformes, can more readily be treated separately. As an entire group they show unmistakable evidence of being derived from a parent stock somewhere intermediate between the Steganopodes and Ciconiae. In the entire order the plumules are uniformly distributed, powder down is present in a few, and the aftershaft is present in all but the Cathartae, which, however, seem otherwise to be the lowest in the evolutionary scale.

I. Suborder CATHARTAE

Pl. 22, Fig. 34

a) *Gymnogyps californianus*

(1) *Remiges*

Barbs moderately broad, but very heavily built, pith of rami more than one cell in thickness. Barbules large, the distals larger than usual relative to proximals. Fewer barbules per unit of

measure than in any group previously studied, about 28 distals and 12 or 13 proximals per millimeter.

Inner vane.—*Distal barbules* (pl. 22, figs. 34a, 34b) with large bases, about 0.4 mm. long by 0.05 mm. wide. Stout base of the distals furnished with moderate, lobate ventral teeth; the pennulum stout, with about 5 stout, progressively longer hooklets, followed by a few long, slender ventral cilia, the distal portion devoid of them. Two basal dorsal cilia developed as in *Plotus*, forming stout, blunt, laterally projecting, spinelike processes; all the other dorsal barbicels rudimentary. Distal to these characteristic dorsal cilia there is a bend in dorsal contour of barbule as shown in the figures. When detached, barbules usually lie in the position shown in plate 22, figure 34b. Proximal barbules (pl. 22, fig. 34c) with relatively small bases, a series of moderate ventral teeth, and pennulum which is broad proximally, but rapidly tapering to fine thread. Pennulum somewhat shorter than base.

Outer vane.—*Distals* (pl. 22, fig. 34d) differ from those of inner vane mainly in possessing larger number of hooklets, in greater development of ventral cilia, and in absence of dorsal ones. *Proximals*, as shown by plate 22, figure 34e, very similar to those of inner vane, but slightly larger, and ventral teeth a little more prominent, at extreme tip becoming slightly more separated from one another and assuming more of a toothlike form. Typical ventral cilia not developed.

b) Other Types

Cathartes aura has practically the same types of barbules, though smaller and the barbicels not so stout. On the broad basal portion of the primaries, the proximal barbules at the tip of the barbs have the ventral teeth transformed into toothlike cilia, but they are not proliferated and do not become slender or hooked.

The back feathers of *Cathartes aura* have barbules resembling those of the outer vane of the remiges, the distals differing in having a very stout heavy pennulum, with fewer and more slender teeth, and with stout appressed ventral cilia. The breast feathers have the barbules very much simplified and reduced. No flexules are ever developed.

c) Down

The down barbules of *Cathartae* are very long and slender, with the nodes only marked by slight enlargements, showing best on the proximal vanule, the internodes being very long. The bases of the down barbules are hardly differentiated from the pennula, being very narrow.

d) Relationships

The Cathartae show many characters in the minute feather structure which appear to show rather close alliance with the Steganopodes, and in one particular, namely in the nature of the distal barbules of the inner vane, show an astonishing likeness to *Plotus*. This is a character which could easily have arisen separately in the two groups, as it undoubtedly has done in other cases, e. g., the Bucerotidae, but the other likenesses between the Cathartae and the Steganopodes as a group make it more probable that *Plotus* and the Cathartae had a common ancestor. As will be shown below, the present group differs considerably from the Accipitres but the gap is bridged to some extent by the Gypogerani and Vulturidae.

e) Summary

The main characters of the Cathartae are as follows:

(1) Barbules relatively widely spaced on the barb, and of large size.

(2) Distals of remiges characterized by large stout base, moderate ventral teeth, heavy pennulum, and a series of progressively longer stout hooklets, followed by a few large, more or less appressed ventral cilia, the dorsal cilia being reduced to 2 stout, blunt, spine-like, basal ones immediately beyond which there is a conspicuous bend in the barbule.

(3) Proximals with moderate base and ventral teeth, pennulum shorter than base, and with no cilia on either inner or outer vane.

(4) Down barbules long and slender, with long internodes and very inconspicuous nodes.

II. Suborder GYPOGERANI

Pl. 22, Fig. 35

Though in general appearance the secretary birds are farther removed from typical Accipitres than are the American vultures, in feather structure they have a much closer resemblance.

a) *Gypogeranus serpentarius*

(1) *Remes*

Inner vane.—*Distal barbules* (pl. 22, fig. 35c) more or less intermediate in form between those of the other suborders of this group. Base and ventral teeth moderate, hooklets 5 in number, and slender as in Falconidae, ventral cilia slender and rather inconspicuous,

and dorsal cilia, except basal two, rudimentary. The latter not so stout or so close together as in the Cathartae but more so than in the Falconidae. *Proximal barbules* (pl. 22, fig. 35*d*) relatively small and of typical falconid type.

Outer vane.—*Distal barbules* differ from those of inner vane in the greater length of the hooklets and in the shorter cells of the pennulum, the latter resulting in the close approximation of the ventral cilia, so that they appear brushlike. Proximal barbules have well-developed, hooked ventral cilia, as in Accipitres.

Distal to the incision of the feather, where vanes are narrowed, distal barbules of inner vane do not possess dorsal barbicels, and proximal barbules of outer vane do not have hooklike ventral cilia. The latter are developed but lie closely appressed to the barbule.

(2) Back Feathers

Gray back feathers of *Gypogeranus* with distal barbules with relatively large pennula, furnished with small, rather weak hooklets and long, slender, closely set ventral cilia. Pigment concentrated in spots, resulting, as in gulls, in bluish tinge in gray color (pl. 22, figs. 35*a*, 35*b*).

(3) Down

The down barbules do not materially differ from those of other Falconiformes, being moderately elongate, reaching a length of 2 mm. or more, the base poorly developed, and pennula very slender with slightly enlarged nodes, which, especially at tip, are furnished with short, inconspicuous prongs.

b) Summary and Relationships

The Gypogerani are much nearer to the Accipitres than to the Cathartae as far as feather structure is concerned. They agree more closely with the Cathartae in the character of the dorsal cilia of the distal barbules of the inner vane, but in all other details of structure they are almost identical with the Accipitres.

III. Suborder ACCIPITRES

The birds of this suborder form a compact, well-defined group, including the hawks, eagles, ospreys, and Old World vultures. The owls used to be associated with this group until further investigation showed that they were in reality widely separated, with many points in common as the result of parallel evolution and similar adaptation. The morphology of the feathers agrees with the osteology, myology, and other characters in showing that the Striges really have nothing in common with the Accipitres as regards near relationship. As in other Falconiformes, the plumules of the Accipitres are uniformly distributed, and in a few forms powder-down is present. The aftershaft is present, and usually well developed.

a) *Buteo borealis*(1) *Remiges*

Shaft about as wide as deep, quadrangular, with well-developed ventral groove. *Vanes* notched or incised on outer vanes, the rami of outer vane beyond point of incision as wide as shaft is deep, the pith more than one cell in thickness, with moderate ventral ridge, with villi on ventral edge. Proximal vanule with over two-thirds as many barbules as distal vanule, there being 28 to 30 distal barbules and 22 to 23 proximals per millimeter, the latter small relative to distals.

Inner vane.—*Distal barbules* (pl. 23, fig. 38a) with long, slender base, about 0.38 by 0.06 mm., with relatively small, but broad and lobate ventral teeth; pennulum much longer than base, with 5 slender, moderately long hooklets, which progressively increase in length, a well-developed series of slender, filamentous ventral cilia, and a series of slender dorsal cilia, the basal ones stouter and more spinelike, but not lobate as in the *Cathartae*. *Proximal barbules* (pl. 23, fig. 38b) with base relatively small as compared with distals, about 0.75 by 0.07 mm., with 4 or 5 short, pointed ventral teeth and moderately slender pennulum, a little over half as long as base.

Outer vane.—*Distal barbules* much like those of inner vane, but base shorter and relatively stouter, pennulum shorter, the hooklets usually 6 in number, and relatively longer, and no dorsal cilia. *Proximal barbules* (pl. 23, fig. 38c) on terminal portion of barbs with a series of highly developed hooked ventral cilia, basal ones, representing ventral teeth, short and triangular, middle ones almost like hooklets of distal barbules, outer ones smaller, weak, and filamentous.

(2) *Other Feathers*

Back feathers have structure differing from remiges chiefly in simplification. Barbules more slender, especially base, all the barbicels considerably reduced and vanules open, i. e., with spaces between barbules, which stand in vertical plane relative to surface of barb (see plate 23, figures 41a and 41b, representing barbules from back feather of *Falco rusticola*). *Breast feathers* similar, but still more simplified, the bases of barbules very elongate and slender and all barbicels greatly reduced.

b) *Other Types*

Examination of a large number of species of different sections of the suborder shows that there is little variation in the form of the barbules. Feathers of species of *Buteo*, *Circus*, *Haliaeetus*, *Archibuteo*, *Spizaetus*, *Haliaeetus*, *Aquila*, *Elanus*, *Falco*, *Pandion*, *Polyborus*, and *Gyps* have been examined, and no striking deviations from the type described have been found. In the distal barbules of *Falco peregrinus* (pl. 23, fig. 36a) the pennulum is rela-

tively short, but the proximals, (pl. 23, figs. 36b, 36c) almost exactly as in *Buteo*. *Falco sparverius*, again, has a long pennulum on the distal barbules. In *Haliaeetus leucocephalus* the pennulum of the distals is short, and the basal dorsal cilia unusually stout (pl. 23, fig. 39a). The proximals (pl. 23, fig. 38b) have longer and more prominent ventral teeth than in *Buteo*. *Polyborus cheriway* agrees with *Haliaeetus* in the small pennulum and spinelike dorsal cilia of the distal barbules (pl. 23, fig. 40a).

The structure of the feathers of *Circus hudsonius* was worked out in detail by me (1914); they agree with *Buteo* in all important details.

In *Gyps fulvus*, representing the Vulturidae, the barbules of the outer vane of the remiges differ considerably from the type, as shown by plate 22, figures 33c and 33d. The distal barbules have enormously developed hooklets and ventral cilia, giving the barbule a very unique appearance. The proximal barbules on the terminal portion of the barbs do not acquire hooked cilia as in other Accipitres, but differ from those of the inner vane merely in the slight proliferation of the ventral teeth, which are only partially transformed into cilia, as shown in plate 22, figure 33d. The back feathers of this species differ from those of more typical accipitrines only in the great width of the pennulum of the distal barbules (pl. 22, figs. 33a, 33b).

c) Down

The down barbules are very variable, even within a single genus. In the majority of the group, e. g., *Accipiter cooperi*, *Pandion carolinensis*, *Circus hudsonius*, *Buteo borealis*, and *Gyps fulvus*, the barbules are elongate and very slender, with very slight swellings at the nodes, and short prongs toward the tip. In *Falco*, however, the nodes are more enlarged, not conspicuously so in *F. rusticola* or *F. peregrinus* but strikingly so in *F. sparverius* where the pigmentation is in deep nodular spots. As shown in plate 35, figure 105, the internodes are very slender and frequently wavy, the latter condition being very unusual in down barbules.

d) Relationships

The microscopic morphology of the feathers of the Accipitres presents many points which are difficult of interpretation. Admitting their relationship with the Cathartae, which seems to be

plainly indicated by other features in their anatomy, and is made rather easy, even taking into consideration the structure of their feathers, on account of the intermediate condition of *Gypogeranus*, the Accipitres must be regarded as derivatives of a Steganopode-like bird. Yet in the form of the ventral cilia of the proximal barbules, and of ventral teeth, hooklets, and dorsal cilia of the distals, they come very close to the Galli. The down of some resembles that of the Steganopodes while that of others, e. g., *Falco sparverius*, resembles that of some Coraciiformes. However, all of these points of resemblances are features which could easily be conceived of as having been developed more than once, and it seems best to regard the Accipitres as derivatives of the Steganopodes through the Cathartae and Gypogerani.

e) Summary

The Accipitres are characterized as follows:

(1) Distal barbules of inner vane of remiges with relatively large base, lobate ventral teeth, 5 hooklets, slender filamentous ventral cilia, and slender dorsal cilia, the basal ones spinelike; pennulum frequently much longer than base.

(2) Distals of outer vane with shorter base, and relatively shorter pennulum with shorter cells, making a brushlike series of ventral cilia.

(3) Proximals of inner vane with relatively small base, short pointed ventral teeth and moderately long pennulum.

(4) Proximals of outer vane, on distal half of barb, with well-developed series of hooklike ventral cilia.

(5) Body feathers differing from remiges only in simplification, and slender form of barbules.

(6) Down barbules very fine and slender, the nodes more or less enlarged, sometimes pigmented.

7. Order GALLIFORMES

Plate 24

Comprising a very large assemblage of the so-called "game-birds," the present order is subdivided into four suborders as follows: (1) *Mesaenatides*, represented only by the kagu or mesite of Madagascar; (2) *Galli*, including the megapodes, curassows, pheasants, partridges, turkeys, etc.; (3) *Turnices*, including the Hemipodes of the Old World; and (4) *Opisthocomi*, to which belongs only the peculiar Hoactzin of South America.

Unfortunately, I have been unable to secure feathers of the first and fourth suborders for examination, and the relationships suggested by their feather structure cannot, therefore, be discussed. The other two groups, *Galli* and *Turnices*, though in superficial appearance very similar, differ in so many details of feather structure that they may more advantageously be considered separately.

I. Suborder GALLI

Pl. 26, Figs. 42-47

Though containing a very large number of species and genera, this suborder forms a fairly compact and well-defined group. In general they are characterized by the restriction of the plumules to the apteria, and by the variability of the aftershaft. In some members of the group, e. g., *Bonasa*, the latter is better developed than in any other group except Casuariiformes, while in others, e. g. *Pavo*, it is very small and almost rudimentary.

a) *Gallus domesticus*

(1) *Remex*

Shaft slightly wider than deep, with a broad, conspicuous ventral groove; *calamus*, in contrast to the condition found in Anseres, short, not greatly inflated, its caliber less than that of the shaft.

Vanes firm, *barbs* of the inner vane set about 18 per centimeter, those of outer vane considerably less, especially in the primaries. *Vanules* with barbules very close set, about 40 distals and 32 proximals per millimeter in a typical portion of the feather, this number of proximals being larger relative to the number of distals than in most water-birds.

Inner vane.—*Distal barbules* (pl. 24, fig. 42a) with base about 0.26 mm. in length by 0.04 mm. in width, the pennulum about the same length. Base rather broad and quadrangular, with usually 3 ventral teeth, these in the form of broad lobes, very thin and film-like. Nuclei in a conspicuously diagonal line, on account of the short, broad form of the base, with its broad ventral teeth. Pennulum with 6 to 8 hooklets of moderate size, progressively increasing in length, not slender with enlarged hooks, as in Anseres, but stouter basally. Ventral cilia of moderate size, not flexible or appressed, but in the form of stout, strongly curved, hooklike processes, decreasing in size toward the tip, but relatively well developed on the whole length of the pennulum; 3 or 4 sharp, spinelike, dorsal cilia, not, however, highly modified as broad lobate or hoodlike projections. More distal cells of the pennulum with short, pronglike, rudimentary dorsal cilia.

Proximal barbules (pl. 24, fig. 42b) with slender base, about 0.6 mm. long by 0.05 mm. wide, with a series of short, pointed, lobate ventral teeth. Pennulum remarkably short, especially on

more basal portion of barb, for the most part not exceeding one-third the length of the base, broad basally, tapering rapidly to a slender but short filament.

Outer vane.—*Distal barbules* (pl. 24, fig. 42c) even shorter than on inner vane, total length under 0.5 mm., the base constituting about one-half of this. Base slightly curved longitudinally, with lobate ventral teeth not as broad as in inner vane. Pennulum with hooklets about as in the inner vane. Ventral cilia more nearly subequal to each other for the whole length of the pennulum, strongly curved, and well separated from each other. Dorsal cilia in the form of short prongs.

Proximal barbules on proximal portions of the barbs closely resembling those of the inner vane, but pennulum even shorter. On the outer portion of the barbs, the proximals (pl. 24, fig. 42d, 42e) with ventral teeth proliferated and transformed into a series of stout, strongly hooked ventral cilia, in some cases almost exactly like hooklets in form, more numerous on more distal barbules, but only 3 to 5 basal ones strongly hooked.

(2) Other Feathers

Body feathers, where there are no special color modifications, merely simplifications of remex type, distal barbules resembling outer vane type, proximals the inner vane type. *Vanes* not firmly interlocking and usually a large portion of feather downy. *After-shaft* with well-formed shaft, its vanes distinct and separate, barbs attached in linear series as in contour feathers, and not tuftlike as is more usual. *Vanules* of the interlocking or pennaceous portion always open, i. e., barbules in a vertical plane and therefore with spaces between them. *Distal barbules* with long, slender bases, with more or less reduced ventral teeth. Pennulum with 3 to 5 short, weakened hooklets followed by a series of the same type of short, curved, inflexible and subequal ventral cilia as in the remiges, these becoming short and more or less rudimentary in looser feathers. *Proximal barbules* (pl. 24, fig. 42f) with elongated, tapering bases, with moderate, rather slender, ventral teeth. Pennulum short, as in remiges, almost invariably considerably less than half length of base; no cilia.

b) Other Types

The minute structure of the remiges is remarkably constant throughout the group, and it is possible to distinguish a gallinaceous bird from all others very easily by the structure of its remiges. The description of the feathers of *Gallus domesticus* will hold, with very slight modification, for all the Phasianidae.

In the Tetraonidae the pennulum of the more terminal proximal barbules of the outer vane has a longer series of ventral cilia, which are relatively somewhat shorter, and of more uniform size. In some members of the family the ventral ridge of the barbs is extremely broad, as in Anserine birds. See plate 24, figures 43a, b, and c.

In the Meleagridae the distal barbules of the remiges have the ventral teeth enormously developed as broad, thin filmlike sheets, while the hooklets are very long and slender, almost as much so as in *Olor*. See plate 24, figures 44a, 44b.

In the Megapodidae and Cracidae, as exemplified by the genera *Megapodius* and *Penelope*, the structure of the feathers is very similar to each other, both varying a little from the usual type. In the remiges of *Megapodius* and *Penelope* the distal barbules (pl. 24, fig. 45a, 46a) are characterized by a rather elongate base, somewhat sinuate in ventral profile, with relatively small ventral teeth. The hooklets and ventral cilia are of typical gallinaceous form, but the dorsal cilia differ in the slightly stouter, more thornlike form of the basal two. The proximal barbules which possess ventral hooklike barbicels (pl. 24, fig. 45b) are restricted to a smaller portion of the tip of the barbs.

The *body feathers*, where there are no special color modifications, undergo a similar simplification and assume a very similar form, in nearly all gallinaceous birds. The aftershaft, when developed, is of the form described for *Gallus domesticus*, with well-developed shaft and distinct separate vanes; the vanes of the main feather plate are always of the open type; the barbules are nearly always at least recognizably similar; the distals with curved, hooklike ventral cilia, the proximals with relatively extremely short pennula.

c) Down

The down barbules of gallinaceous birds differ considerably on different portions of the barbs, and to some extent on different barbs (see Part I, p. 270), but reach their highest and most typical development on the basal portion of the distal vanule of the well-developed down barbs of the main feather plate.

These typical barbules (pl. 36, fig. 108) are readily distinguishable from those of any other group of birds. They are densely set, sometimes as many as 50 per millimeter on each side near the base of the barbs, though always considerably less at the middle and tip. They are usually extremely long, reaching a length of over 5 mm. in various species of pheasants and turkeys, though as a rule they are more nearly 3 mm. in length. The base of these barbules is only slightly differentiated. The pennulum on its more proximal portion has poorly developed swollen nodes (pl. 36, fig. 108b), which, however, soon increase in size and develop a typical

ringlike form (pl. 36, fig. 108c). Some of these rings frequently, in fact almost always to a greater or less extent, break loose from the nodes, and slide along on the slender, filamentous barbule like rings on a wire, sometimes breaking up into groups of 5 or 6. It is possible to move them along on the barbules by placing them on a slide and moving the cover glass. Toward the tip of the barbules the ringlike structure is again lost, and the nodes become simply swollen. On the proximal vanule these rings are usually not so perfectly developed, and on the more distal portion of both vanules the nodes become simply swollen, and shaped more or less like a eucalyptus seed, with short prongs, or the barbule becomes almost smoothly filamentous, with indistinct nodes. The outside diameter of the rings in *Meleagris virginiana*, for instance, is about 0.012 mm., while that of the internodes of the barbules is only 0.004 to 0.005 mm. The down at the base of remiges and rectrices, and that of the aftershafts, never possess the ringlike structure. The downy structure varies very little in any of the families of the suborder.

d) Color Modifications

There are many interesting color modifications in this group, especially in the Phasianidae, but they can only briefly be discussed here. White is usually produced by diffusion of light merely from translucent barbules, but in *Lagopus* the barbules (pl. 24, fig. 47a) are filled with minute bubbles which tend further to diffuse the light. Deep glistening red, yellow, and orange colors are usually produced by pigmented, highly polished barbs which are naked, or possess much reduced barbules. Changeable metallic lilacs, fiery reds, blues, greens, and purples are produced by highly refrangent, simple, rodlike barbules, the silvery blue feathers of *Phasianus torquatus*, for example, being a result of the combination of white barbs with rodlike blue barbules. In the coherent green vanes of the tail feathers of roosters, and other similar feathers, the pennula of the distal barbules (pl. 24, fig. 42g) are responsible for the color as in the Anseres, the individual cells, however, not being demarcated by constrictions, but the whole pennulum in the form of a curved, spoonlike structure (pl. 24, fig. 42f).

There is a very unusual condition found in the blood-red breast feathers of the golden pheasant, where the barbs are closely appressed and brought to lie almost parallel with the shaft. In these feathers two barbs frequently fuse to form a single one at a short distance

from the shaft, which remains single for all the rest of its length. In one case the barb was seen to be split for only a portion of its length, being fused into one at both base and tip.

In peacocks the highly iridescent blue, green, and bronze colors are the result of barbules which are totally metamorphosed in both base and pennulum to produce color.

e) Relationships

According to the feather structure, the Galli are highly specialized birds, the broad, ventral teeth of the distal barbules, the hooked ventral cilia of the proximals, and the nature of the down, being specializations and decidedly not primitive characters. The form of both distal and proximal barbules, as well as the form of the down, shows unmistakable affinity to that of the Columbæ on the one hand, and the Cuculiformes on the other, the so-called "Peristeropode" group (Megapodidae and Cracidae) more strongly suggesting the cuculoid birds, while the "Alectoropodes" (pheasants, grouse, etc.) are reminiscent of the Columbæ. (Compare plates 24, 29, and 30.)

Unmistakable relationship is also shown to the Tinami, which, according to feather structure, should be considered as a specialized offshoot from a primitive gallinaceous stem. This will be more fully discussed under *Crypturiformes*.

In some respects, namely in the form of the barbicels of the distal barbules of the remiges, some affinity to the Rallidae and other gruiform forms is shown, but the nature of the body feathers is totally different, and it is more probable that the few striking similarities are rather to be interpreted as the result of parallel evolution. (Compare plate 24 with plate 25.)

The relationship of the Galli with the Turnices will be discussed under the latter.

f) Summary

The Galli are characterized as follows:

- (1) Plumules only in apteria.
- (2) Aftershaft variable, but when developed, with distinct and separate vanes.
- (3) In remiges, proximal barbules small as compared to distals, and both series very close set.

(4) Distal barbules of remiges short, the bases short with large, thin, lobate ventral teeth, the pennula with a long series of progressively longer hooklets, a complete series of curved, inflexible, ventral cilia, and in the inner vane a series of little-specialized, spiny, dorsal cilia.

(5) Proximal barbules of inner vane with moderate bases with short, pointed, ventral teeth, and with very short pennula.

(6) Proximals of outer vane, on distal portion of barbs, with a highly developed series of stout, hooked, ventral cilia, sometimes very closely resembling hooklets.

(7) Barbules of body feathers differing from remiges only in simplification of structure, no flexules ever developed.

(8) Down, where typically developed, with extremely long, slender barbules, with detachable, ringlike structures at the nodes.

II. Suborder TURNICES

Pl. 24, Fig. 48 -

The Hemipodes, or bustard quails, belonging to the two rather divergent genera *Turnix* and *Pedionomus*, are small, quail-like ground birds of the southern parts of the Old World. They constitute a rather isolated group whose place in the system of classification has been in considerable doubt.

a) *Turnix lepurana*

(1) *Remez*

Feather small, the wing being somewhat reduced in size; *shaft* with slight ventral groove; *barbs* not deep, the ventral ridge narrow.

Inner Vane.—*Distal barbules* (pl. 24, fig. 48a) small, base about 0.2 mm. long by 0.03 mm. wide, tapering conspicuously to ventral teeth, which are relatively smaller than in *Gallus*, otherwise very similar; nuclei in conspicuously diagonal line. Pennulum distinctly galline in form, slightly longer than base. Hooklets rather short, usually 5 in number. Ventral cilia not well developed except immediately distal to hooklets, as in Ardeae, of distinctly galline and not ardeid form, however. Dorsal cilia, except basal two, in form of short prongs as in Galli, but basal two larger and thorn-like in form (pl. 24, fig. 48a). *Proximal barbules* (pl. 12, fig. 48b) moderately slender, base and ventral teeth as in Galli, pennulum very slender and filamentous, almost equal to base in length.

Outer vane.—*Distal barbules* very similar to those of inner vane, but with 6 hooklets, and no dorsal barbicels, and never more than 3 well-developed ventral cilia. Proximal barbules of basal and middle parts of barb like those of inner vane, but pennulum much shorter, much as in Galli. Towards tip of barb, ventral cilia developed almost exactly as in Tetraonidae.

(2) *Other Feathers*

Back feathers rather loose-vaned. Aftershaft with long shaft and distinct vanes, but barbs much farther apart than in Galli, therefore not such a compact structure. Barbules much simplified. Distals with elongated, slender base, with reduced ventral teeth; pennulum greatly elongated and threadlike, three times length of base on basal portion of barb, 4 short, rather weak teeth, and 2 or 3 short, blunt ventral cilia immediately beyond hooklets. Proximals, near base of barb, with slender but well-formed base, 4 or 5 short but slender and sharp ventral teeth, and greatly elongated pennulum. Towards tip of barbs, pennula shortened, and barbules greatly reduced and simplified.

Breast feathers very similar, but pennula on basal barbules not so elongate. Aftershaft weaker.

b) Down

The down is distinctly different from that of the Galli. Ringlike structures are never developed at the nodes, the latter being inconspicuous and only slightly enlarged, and never pigmented, although the internodes have black pigment. The length of the barbules is moderate, seldom reaching over 2 mm.

c) Relationships

The structure of the distal and proximal barbules of the remiges, while strikingly galline in some respects, is likewise very similar, in fact more so, to *Eurypyga*. The structure of the down, which has such a strikingly characteristic development in the Galli, in these birds is totally different, but is almost exactly the same as that of *Eurypyga*. It might be suggested that the Gruiformes and Galliformes are divergent branches of a common primitive stem, and that the Turnices and *Eurypyga* are to be considered as more or less nearly related early offshoots either from the gruiform or galliform branch, thus exhibiting somewhat intermediate characters.

d) Summary

The Turnices are characterized as follows, in common with the Galli:

- (1) Plumules sparse, restricted to apteria.
- (2) Aftershaft present, with long shaft and distinct vanes.
- (3) Distal barbules of remiges with broad bases, with broad, thin ventral teeth and strikingly diagonal line of nuclei; pennulum with

short, stout hooklets and short, curved, inflexible ventral cilia, but only the proximal ones developed.

(4) Proximal barbule with base moderate and ventral teeth well developed but not conspicuous, those of distal part of barbs of outer vane with well-developed series of ventral cilia, the proximal one hooked.

(5) Barbules of back and breast feathers mere simplifications of remex type.

In the following characters they differ from typical Galli: (1) poor development of barbicels on terminal part of pennulum and stout, thornlike form of first two dorsal cilia of distal barbules; (2) rather long, filamentous pennulum of proximal barbules; and (3) moderately long down barbules with slightly enlarged unpigmented nodes, the internodes with black pigment.

8. Order CRYPTURIFORMES

Plate 25

This order, which includes the aberrant South American tinamous, has in some ways the most specialized feather structure of any existing birds. They form a compact group of some forty species, all in the family Tinamidae. They differ from all other birds in having plumules present between the contour feathers, while absent in the apteria. The aftershaft is rudimentary or absent in some genera but large and well developed, with distinct vanes, in other genera (e. g., *Rhynchotes*). Although strictly ground birds which can fly very poorly and have a remarkable lack of control of the flight powers they do possess, the small wings have remiges which are very well developed.

a) *Tinamus solitarius*

(1) *Remex*

Calamus short and of smaller caliber than shaft. *Shaft* slightly wider than deep, with small median groove. *Vanes* extremely firm and elastic, the *barbs* adhering to each other with remarkable tenacity. *Rami* not deep, the ventral ridge rather narrow; about 25 per centimeter on each side basally, 16 to 18 for greater part of feather.

Inner Vane.—*Distal barbules* (pl. 25, fig. 49a) relatively very small, base very short and broad, about 0.35 mm. long by 0.04 wide, the ventral teeth broad, lobate, and filmlike. Pennulum, in side view, of peculiar shape, narrow in hooklet region, then becoming very broad (about 0.15 mm.) and thence tapering evenly to tip.

Hooklets short, subequal in length, and extremely numerous, usually 8. Proximal 3 or 4 ventral cilia moderate, not curved, more or less appressed, more distal ones rudimentary. Dorsal cilia strikingly similar to neural spines of dorsal vertebrae of a dog, in relative size, shape, and general direction, the first two or three rapidly increasing in size, and progressively pointing more distally, the remaining ones slowly decreasing again but continuing to project at a smaller and smaller angle. *Proximal barbules* unique (pl. 25, fig. 49b). Bases about 0.5 mm. long by 0.05 mm. wide, very much curved transversely, so that dorsal part lies almost parallel with ventral part, a device taking the place of a dorsal flange. *Pennula completely fused into a solid bar lying parallel with ramus*, the ventral teeth, one or two in number, projecting ventrally just proximal to the bar; dorsal teeth absent. Hooklets of distals hook under recurved dorsal edge of proximals, and fused pennula of latter prevent their slipping out under strain.

Outer Vane.—Structure of *distal barbules* exactly same as in inner vane, except the less development of more basal dorsal cilia (pl. 25, fig. 49c). Outer bar formed by fusion of pennula of proximals same as on inner vane for over nine-tenths of vanule, the proximal barbules of the distal 2 or 3 millimeters with well-developed, strongly hooked barbicels on free pennulum, as in Galli.

(2) Other Feathers

The *back feathers* with distal barbules with rather elongate, rectangular base, ventral tooth single, much reduced, pennulum with broad face in nearly same plane as base, hooklets reduced to 3 or 4, other barbicels short, blunt, and more or less rudimentary (pl. 25, fig. 49d). Proximal barbules differing only in having a narrower base, which stands vertically, the bar of fused pennula carried to very tip on both vanes in well-developed feathers (pl. 25, fig. 49e). In looser ones, and in *breast feathers*, pennula of proximal barbules imperfectly fused on distal half of barb, and on distal third no fusion whatever. Distal barbules of breast feathers like those of back feathers, except that pennulum has long filamentous tip.

b) Other Types

All species of tinamous are strikingly similar in the structure of their feathers. The remiges of *Nothocercus frantzii*, for instance, differ only in the slightly longer pennulum of the distal barbules, and the more restricted area of free barbicelled proximals on the outer vane. The back and breast feathers have been examined in different species of five different genera (*Nothocercus*, *Tinamus*, *Rhynchotus*, *Nothura*, and *Calopezus*), and in all the structure of the barbules is remarkably similar, differing only in the relative length of the pennula of the distal barbules, development of ventral , etc.

c) Down

The downy structure in *Calopezus* and *Nothura* is *exactly* the same as in typical gallinaceous birds, not only in the structure of the typical basal barbules of the distal vanule, which have detachable rings of the same form, but also in the method and degree of simplification in other parts of the barbs. In *Tinamus* and *Nothocercus*, on the other hand, the detachable rings are only slightly developed, but the more basal nodes are very much enlarged, while the more distal ones are in the form of tiny droplets, the type of barbule thus resembling that of the Columbæ very closely (pl. 25, fig. 49f). In all species the down barbules are very long, as in typical gallinaceous birds.

d) Relationships

The structure of the down alone is sufficient proof that the tinamous are unquestionably far more closely allied to the Galli than to any other birds, since it is difficult to believe that the peculiar detachable rings at the nodes would be developed twice, by separate paths of evolution. The remarkable similarity of the down of some species to that of the Columbæ can more readily be thought of as parallel evolution, since it is a type which recurs again in the Rhamphastidae, for instance, and is very easily derived from the gallinaceous type of structure. The occurrence of these two types of down in this single order, however, is suggestive of the fairly close relationship of the *Columbæ* and *Galli*.

The Crypturiformes show a remarkable number of specializations of feather structure which are absolutely peculiar to them; in fact, it may safely be said that the barbs of tinamous have the most perfect and highly specialized interlocking mechanism found anywhere in birds. This fact alone is enough to show the error of grouping them with the Ratitæ, or even anywhere near them. They must undoubtedly be looked upon as a highly modified offshoot from the Galliformes, if the feather structure be taken into account at all.

e) Summary

Crypturiformes are characterized as follows:

- (1) Plumules sparse, and found only between contour feathers.
- (2) Aftershaft present, often rudimentary, when well developed with long shaft and distinct vanes.

(3) Distal barbules of inner vane of remiges with very short, relatively broad base, with broad, lobate ventral teeth; pennulum widest immediately beyond hooklets, thence tapering in either direction; hooklets excessively numerous, subequal, about 8 in number, only proximal ventral cilia developed, these moderate and more or less appressed, dorsal cilia in shape, relative size, and angle of projection resembling the series of neural spines of dorsal vertebrae of a dog.

(4) Proximal barbules of inner vane of remiges with base concave toward distal side, the recurved dorsal portion replacing the flange in other birds; pennula fused into a solid outer bar, lying parallel with ramus.

(5) Distal barbules of outer vane differing from those of inner only in reduction of dorsal cilia; proximal barbules on over nine-tenths of barb like those of inner vane, with pennula fused into a bar, but on short distal portion free, with well-developed hooked barbicels as in *Galli*.

(6) Structure of body feathers a mere simplification of that of remiges, pennula of proximals still fused.

(7) Down of two types, exactly like that of typical *Galli* in *Calopezus* and *Nothocercus*; closely resembling that of *Columbae* in *Tinamus* and *Nothura*.

9. Order GRUIFORMES

Plates 26 and 27

Constituting a very heterogeneous group of birds whose relationship has always been considered more or less doubtful, but affording a convenient resting-place for many birds *incertae sedis*, the present group shows so many variations among themselves in feather structure, and the different types included approximate so many other groups, that practically no general epiphylogenic characters which are common to all can be described. The plumules in some are generally distributed, in others sparse all over, in *Otis* confined to the apteria. The aftershaft is present, rudimentary, or absent in different species, but never, so far as I have been able to find, with well-developed shaft and distinct vanes.

a) *Grus canadensis*

(1) *Remea*

Shaft about as wide as deep, very rectangular in cross-section except for short distance distal to superior umbilicus; at superior

umbilicus very high, much higher than wide, and egg-shaped in cross-section. *Rami* moderately broad at junction with shaft, pith more than one cell thick, the ventral ridge rather narrow, less than one-seventh total width of ramus, its ventral edge smooth.

Inner vane.—*Distal barbules* (pl. 26, fig. 50a) set about 28 per millimeter. Base short and broad, about 0.24 mm. by 0.06 mm., ventral teeth of moderate size, broad and lobate, their tips often inconspicuously jagged, or very slightly bifurcated. Pennulum considerably longer than base, rather broad, hooklets 5 or 6, moderately slender and progressively longer, but hooklet cells so short, and each successive hooklet curved so much farther distal, that distal ones reach no farther ventral than proximal ones; ventral cilia slender, but slightly curved, all but first two or three appressed to pennulum; more proximal dorsal barbules spinelike, especially first two, more distal ones well developed, but slender, curving forward. *Proximal barbules* (pl. 26, fig. 50c) relatively large, set about 17 per millimeter, base about 0.73 mm. long by 0.07 wide, with 5 or 6 rather narrow, pointed, conspicuous ventral teeth; pennulum somewhat shorter than base but over half as long, flattened and moderately broad proximally, its tip slender, with rudimentary barbicels.

Outer vane.—*Distal barbules* (pl. 26, fig. 50b) differing from those of inner vane only in loss of proximal dorsal cilia, other details of both base and pennulum similar to those of inner vane. Proximal barbules (pl. 26, fig. 50c), except at tip of barb, exactly similar to those of inner vane. Towards tip of barb ventral teeth become separated, and assume shape similar to those in *Butorides* (pl. 20, fig. 21b), i. e., short curved barbieels, intermediate in form between typical ventral teeth, as exemplified in more basal proximal barbules (pl. 26, fig. 50c), and typical hooked ventral cilia, as in the terminal proximal barbules of the outer vane in *Rallus* (pl. 26, fig. 52c).

(2) Other Feathers

Back feathers have distal barbules with rather elongate, slender base, the ventral teeth with bifurcation or jaggedness of tips more pronounced. Pennulum very long, 0.05 mm. or over, giving velvety effect to feathers. Both dorsal and ventral cilia similar to those of distal barbules of inner vane of remex. Proximals (pl. 26, fig. 50d) with slender base, about 0.65 mm. long by 0.05 wide, ventral teeth reduced in size and number, and pennulum relatively shorter than in remiges.

Scapular feathers especially modified as ornamental plumes, a large part of outer vane, and some of inner vane, with discrete, i. e., non-adhering, barbs, which curve outward. This condition is accomplished merely by the breaking off of distal barbules immediately beyond base, thus destroying interlocking apparatus. Tips of proximal barbules also usually imperfect.

Breast feathers have structure of barbules on basal two-thirds of middle barbs very similar to back feathers, except reduction of all barbicels of distal barbules (pl. 26, fig. 50e) and shortening of pennulum of proximals. On distal third a rather sudden transition occurs in both kinds of barbules to type shown in plate 26, figure 50f. No differentiation between base and pennulum, the

barbule evenly tapering for whole length, dorsal edge with complete and continuous series of flexules and dorsal cilia, ventral edge with rather short, slender, more or less appressed ventral cilia. More distal barbs have this structure for three-fourths of their length.

b) Other Types

The structure of the feathers in all species of *Grus* is probably very similar, and there is a similar freeing of the barbs of the terminal part of the scapular feathers in nearly all, if not all, of the species.

In the *Rallidae* the structure of the feathers differs in some important details, approaching more closely to that of the *Limicolae*. In the remiges of *Rallus obsoletus*, the proximal and distal barbules are more numerous, being about 26 and 37 per millimeter respectively. The distal barbules (pl. 26, fig. 52a) have a relatively long base, about 0.25 mm. long by 0.035 mm. wide, becoming very narrow proximal to the small, fingerlike ventral teeth, a condition exactly similar to that in the *Limicolae*. The pennulum is rather narrow except in the hooklet region, the hooklets 5 in number, and slender, and the cilia, both ventral and dorsal, very similar to those in the *Limicolae* (compare plate 26, figure 52a, with plate 28, figure 57a.) The proximal barbules (pl. 26, fig. 52b) have relatively small bases, about 0.5 mm. long by 0.04 mm. wide, with ventral teeth moderately developed, while the pennula are shorter than the bases, and flattened. On the outer vane the distal barbules show no especially interesting characters, but the proximal barbules (pl. 26, fig. 52c) on the distal half of the barb have pennula longer than the bases furnished with a highly developed series of ventral cilia, of which the more proximal ones are hooked. In this character the rails differ from both the *Limicolae* and *Gruidae*. In *Cresicus* the ventral cilia of the proximal barbules of the outer vane are less hooked, while in *Gallinula*, although the pennulum is very long and is sharply bent with respect to the base, as in *Rallus*, the ventral cilia, except two or three basal ones, are not developed.

In the *body feathers* of *Rallus obsoletus* (also of *Cresicus*, *Gallinula*, and other species of *Rallus*) the structure of the feathers is strikingly peculiar, even at the very base of the barbs. As shown by plate 26, figures 52d, e, and f, the distal barbules, from base to tip of the barb, change from a form with three weak hooklets and rudimentary flexules and cilia, to a form with no differen-

tiation between base and pennulum, no ventral barbicels whatever, and a series of very highly developed flexules and dorsal cilia, in a continuous series after the hooklets are lost. Plate 26, figures 52*e* and *f* shows the tardiness of the hooklet cells to develop any dorsal cilia. Plate 26, figures 52*g* and *h* show the method of transformation of the proximal barbules, the distals and proximals being exactly the same on the distal half of the barbs.

In the Aramidae, as typified by *Aramus giganteus*, the barbules of the *back feathers* closely resemble those of the back feathers of the Coraciidae and Megapodidae in that in the distal barbules of the undisturbed vanules the bases are twisted in such a way that although at the junction with the ramus they stand in a vertical plane, they lie in a horizontal plane for most of their length. The distals also resemble somewhat the "peristeropode" Galli in the curved form of the ventral cilia (compare plate 26, figure 51*a*, with plate 24, figures 45*a* and 46*a*). The proximals (pl. 26, fig. 51*b*) also approach the condition in these birds in their elongate tapering bases, and very short pennula. The breast feathers have barbules which resemble those of rails in the great development of the dorsal series of barbicels, consisting of both flexules and dorsal cilia, but are a little closer to those of the cranes in that they are elongate, and possess a highly developed series of ventral as well as dorsal cilia (pl. 26, fig. 51*e*). Plate 26, figures 51*c* and *d* show the distal and proximal barbules respectively at the base of a barb of a breast feather, showing the method of development of the peculiar type shown in figure 51*e* of the same plate.

In *Otis tarda*, representing the Otididae, the remiges are characterized by the remarkable width of the pithy part of the ramus. On the inner vane, on barbs not over about 6 cm. long, the ramus, near its base, is about 1.5 mm. wide, of which the ventral ridge forms a very narrow edge, being less than 0.05 mm. wide. The distal barbules of the remiges are peculiar in their being relatively short, with stout bases and very large, lobate ventral teeth, and exceedingly long hooklets, usually seven in number. They are devoid of conspicuous basal dorsal cilia even on the inner vane. The proximal barbules (pl. 27, fig. 53*b*) have a relatively large base, with a rather stout, moderately long pennulum. The back feathers are distinctly like those of galline birds in the structure of their barbules, the distals having both base and pennulum shaped as in the back feathers of *Gallus*, and the nuclei distinct in the

pennular as well as basilar cells (compare plate 27, figure 53c with plate 24, figure 47a). The proximal barbules, though resembling the Galli in the diagonal line of conspicuous nuclei, differ in the long, slender pennulum (pl. 27, fig. 53d).

Psophia viridis, representing the Psophiidae, has barbules which come very close to the peristeropode Galli, as will be seen by comparing plate 27, figures 54a, b, c and d with the figures of barbules of *Megapodius* and *Penelope* (plate 24, figures 45a and b and 46a). The iridescent golden green of a part of the outer vane of the coverts is produced by refrangent barbules which are completely metamorphosed to serve in color production. In form, on both distal and proximal vanule, they are somewhat shortened, with no barbicels whatever, as shown in plate 27, figure 54e. A short distance from their junction with the ramus they are bent suddenly outward, and from this point, which is the widest, they taper evenly to the tip. Both upper and lower surfaces refract light.

Eurypyga helias, representing the Eurypygidae, also has barbules which show an approximation to the type found in peristeropode Galli, but show a more striking similarity to the Ardeae. As shown in plate 27, figures 55a and c, the general form of the distal barbules is remarkably like that of *Ardea* (compare plate 20, figs. 20a and c), but the size and form of the ventral teeth and ventral cilia are nearer to the megapodes. The proximal barbules (pl. 27, fig. 55d) show a still closer similarity to the Ardeae in the form of the base and in the slender filamentous pennulum, and in the fact that no ventral cilia are developed on the proximal barbules of the distal part of the barbs of the outer vane (compare plate 27, figures 55b and d, with plate 20, figures 20b and d).

Cariama cristata, of the family Cariamidae, very much resembles *Eurypyga* in the details of its feather structure, as shown by plate 27, figures 56a and c, representing a distal and proximal barbule respectively from a back feather.

c) Down

In *Grus canadensis* the down barbules are from 1.5 to 3.5 mm. long, in the form of almost unmodified threads, which, however, under high magnification show small prongs at the nodes, usually two of unequal size, and appressed and inconspicuous. The barbules show a tendency to scuff off, or become chafed, so that small fragments may frequently be seen hanging from them.

In the Rallidae the down barbules are short, stout, and deeply pigmented, with short internodes. The pigment is present chiefly in the distal part of the internodes, the minute prongs and the proximal part of the internodes being more or less unpigmented. In *Rallus obsoletus* (pl. 36, fig. 107) the internodes reach a length of about 0.035 mm. In *Gallinula* the nodes are farther apart, while in *Cresicus* they are nearer together. In *Psophia* the down is black, as in *Rallus*, but the nodes are indistinct, and the pigment almost uniformly distributed. *Eurypyga* (pl. 36, fig. 106) has barbules which are more elongate and slender, very similar to that of the ardeid forms which have dark down, e. g., *Botaurus* (pl. 34, fig. 100). *Aramus* agrees with the cranes in the structure of its down, except that the barbules are not so slender. *Cariama* has down which is very long and filamentous, with enlarged nodes in all except the more basal barbules. In general the structure seems to be more like that of the Ardeae than like that of any other group. The down of *Otis* in the general form of the barb and vanules and length of barbules, is of galline type, but the minute structure is very different, the nodes being entirely undeveloped, and the barbules being merely long, slender, unmodified threads.

d) Relationships

As previously stated, the Gruiformes include a rather heterogeneous assemblage of birds which show affinities to a number of other groups, but are so generalized in some respects and specialized in others as to be very difficult to classify. The rails show a striking affinity, as far as their feather structure is concerned, to the Laro-limicolae. The cranes, on the other hand, differ from the Laro-limicolae, but agree with the Ciconiae, in the form of the proximal barbules of the outer vane of the remiges, which have no ventral cilia, while they agree with the Laro-limicolae, but differ from the Ciconiae, in possessing flexules on the breast feathers. *Aramus*, in the structure of its breast feathers is more or less intermediate between the rails and the cranes, while in its back feathers it approaches the peristeropode *Galli*. *Psophia* also shows characters which are reminiscent of the megapodes and curassows, while *Otis* comes closer to the alectoropode type in the form of the barbules and barbicels. *Eurypyga* shows so many ardeid characters in the structure of its feathers that it strongly suggests its affiliation

with the herons instead of with the cranes. *Cariama* is undoubtedly nearer to *Eurypyga* than to any other forms.

In general it seems best to consider the Gruidae, Aramidae, and Rallidae as offshots from a primitive stem leading to the Laro-limicolae, while the Otidae, Psophiidae, and possibly the Aramidae, are more probably early offshots from the stem leading to the Columbidae and Galli. The Eurypygidae, and possibly the Cariamidae, are almost certainly of ardeid derivation.

e) Summary

(1) Distribution of plumules variable, uniformly distributed, or sparse all over, confined to apteria in *Otis*.

(2) Aftershaft present, rudimentary, or absent.

(3) Distal barbules in different forms showing affinities to the Laro-limicolae, Galli and Ardeae; proximal barbules with inconspicuous teeth, pennulum very different in different forms, sometimes with cilia in outer vane, sometimes without.

(4) Breast feathers in Gruidae, Aramidae, and Rallidae with flexules on barbules, but of galline type in Psophiidae and Otidae, and ardeid in Eurypygidae and Cariamidae.

(5) Down barbules medium or long, smoothly filamentous, or with inconspicuous prongs at the nodes, or pigmented, with the nodes slightly enlarged.

10. Order CHARADRIIFORMES

Plates 28-29

Including a very large assemblage of birds which in general appearance seem to have little or nothing in common, the Charadriiformes are nevertheless joined together into a more or less natural group by numerous more or less intermediate species which bridge over the gaps separating the more widely divergent forms. It is divisible into two main suborders, the Laro-limicolae and Pteroclo-columbae, which will be separately treated.

Suborder LARO-LIMICOLAE

Plate 28

This suborder includes three groups of birds, the Limicolae, the Lari, and the Alcae, including the plovers and their allies, the gull-like birds, and the auks and murres respectively. They are all characterized by the uniform, though often sparse (especially in the

Limicolae) distribution of down, and the presence of an aftershaft, usually well-developed, but in a few cases very small. As was done by Gadow (1891), the Limicolae are regarded as the center of the entire charadriiform group, since in the structure of their feathers as well as in other regards, they are neither the least nor the most specialized. It is for this reason that a limicoline bird was selected for special description.

a) *Numenius americanus*

(1) *Remes*

Calamus and basal portion of *shaft* rather slender, much deeper than wide, the calamus relatively long, the shaft if anything deeper than wide for most of length, with narrow ventral groove and distinct striations on side at junction of barbs. *Rami* relatively deep, the ventral ridge moderately developed, with a smooth ventral edge in both inner and outer vanes. Distal and proximal vanules with 30 and 20 barbules per millimeter respectively.

Inner vane.—*Distal barbules* with relatively broad base (0.28 by 0.056 mm.), subnuclear area especially broad and filmlike, its ventral contour line conspicuously curving in proximal to ventral teeth (pl. 28, fig. 57a). Ventral teeth remarkably small and inconspicuous, both short and narrow. Pennulum slightly longer than base; hooklets 5 or 6 in number, short, moderately slender, the distal ones not conspicuously longer than proximal ones, the hooklet cells not being short and crowded; ventral cilia developed on whole length of pennulum, proximal 2 or 3 short, the more distal ones longer, but appressed to barbule for part of their length (see figure); two proximal dorsal barbules stout, spiny, best described as earlike; more distal ones decreasing in size, and rather rudimentary. *Proximal barbules* (pl. 28, fig. 57b) with very slender base, about 0.5 by 0.04 mm., ventral teeth short, blunt and inconspicuous; pennulum much shorter than base, moderately stout proximally, tapering to fine point.

Outer vane.—*Distal barbules* with bases considerably longer and more slender, about 0.32 by 0.04 mm., the subnuclear area being the part especially reduced (pl. 28, fig. 57c). Ventral teeth somewhat longer but even more slender than on inner vane. Hooklets 5 or 6, longer than on inner vane, almost all of equal length. Series of ventral cilia complete, these barbicels of moderate length, slightly curved, and subequal. Dorsal cilia absent except near tip where a few short rudimentary ones are developed. *Proximal barbules* for over three-fourths of length of barb similar to those of inner vane, but on terminal part of barb ventral teeth proliferating and developing into straight, unhooked ventral cilia (pl. 28, fig. 57d).

(2) *Other Feathers*

Back feathers.—Structure of distal barbules (pl. 28, fig. 57e) much like that of those of outer vane of remiges, but base of some-

what different shape, as shown in figure, hooklets reduced in number and strength, pennulum considerably longer, ventral cilia more curved and more nearly subequal, and dorsal cilia better developed, short and spinelike. Proximal barbules with tapering base and relatively short, stout pennulum, less than half length of base.

Breast feathers similar to those of back in greater part of barbs, but less developed, bases of barbules narrower, hooklets weaker, and weaker ventral cilia. On distal third of barb, barbules (pl. 28, fig. 57f) have a series of highly developed flexules, less curved ventral cilia also being present. These barbules are then not unlike the outer barbules on barbs of breast feathers of *Gavia* (pl. 16, figs. 8e, 8f). The distal and proximal barbules on the distal third of the barb are alike except that the proximals are slightly longer.

b) Other Types

Many species of Charadriidae, including nearly all the genera represented in Western North America, were examined, and all of them were found to be extremely similar in their general feather structure to that of *Numenius*. A barbule from the distal third of a breast feather of *Phalaropus fulicarius* is represented in plate 28, figure 59a, and a comparison with figure 57e of the same plate shows how similar they are, though the stouter form of the flexules and less conspicuous ventral cilia of *Phalaropus* is reminiscent of the rails.

In *Parra spinosa*, or jaçana, representing the Parridae, there is a little modification of the charadriid type in the back feathers, those on the basal half of the barb (pl. 28, fig. 58a) being slightly more elongate and slender, while on the distal half flexules are developed very much as in the breast feathers, but the barbule is not so shortened (pl. 27, fig. 58b).

In *Oedicnemus* the remiges are very much like those of Charadriids in structure, but the breast feathers differ in that flexules are very poorly if at all developed.

Cursorius gallicus, representing the Glareolidae, seems to show in its feather structure a closer likeness to the Ardeae than to the Limicolae. As shown by plate 28, figures 60a and b, both distal and proximal barbules are decidedly like those of the herons. The terminal distal barbules of the breast feathers differ widely from those of all other members of this suborder as shown by plate 28, figure 60c, more closely approximating the herons or storks in the short blunt barbicels.

The Laridae, representing the second group, composed of strong-

flying fish-eaters, differ so little from typical limicoline birds that a special description of their feathers would be superfluous here. Comparison on plate 28 of figures 61*a*, *b*, *c*, *d* and *e*, with figures 57*a*, *b*, *c*, *d* and *e* respectively, will make the similarity strikingly clear. It is interesting to note that the bluish-gray colors of gulls are produced by an uneven distribution of pigment in the barbules, as shown by the figures of *Larus occidentalis* (pl. 28, figs. 61*a*, *d*). In lighter-colored gulls, such as *Larus argentatus*, the light spaces between the dark bars in the bases of the barbules are more extensive. Terns and jaegers have an even distribution of pigment in the barbules. In the former, as exemplified by *Sterna maxima*, the outer vane of the remiges has a hoary appearance due to the great length of the pennula of the distal barbules, which have exceedingly numerous and slender ventral cilia (pl. 28, fig. 62*a*).

The auks, guillemots, murres, etc., representing the Alcidae, seem, according to their feather structure, to form a sort of connecting link between the Colymbiformes and Laridae. The resemblance of the structure of the remiges to that of both the gulls and grebes is well brought out by a comparison of plate 28, figures 63*a*, *b* and *c*, representing barbules of the remiges of *Uria troille*, with figures 61*a*, *b* and *c* of the same plate on the one hand, and plate 16, figures 9*a*, *b* and *c* on the other.

The structure of the breast feathers is remarkably similar to that of grebes and Sphenisciformes. The more basal distal barbules (pl. 28, fig. 63*d*) could very readily be mistaken for those of *Aechmophorus* (pl. 16, fig. 9*e*). The middle part of the barb is furnished with twisted barbules and is exactly similar to that shown in plate 16, figure 9*h*, while on the more distal third the barbules (pl. 28, figs. 63*e*, 63*f*) are strikingly similar to those developed in the outer portion of the barbs of breast feathers of loons (pl. 16, figs. 8*e*, 8*f*).

c) Down

In the Charadriidae the down barbules are quite different in different forms, usually of rather moderate length, i. e., from 1 to 2 mm. long, sometimes pigmented. The nodes are always swollen and more or less distinct, in pigmented types often very distinct with the pigment present in it as a dark spot, almost as in passerine birds (pl. 37, fig. 114). In *Cursorius* the barbules are of this type, and unusually dense, there being as many as 70 barbules per millimeter on each side.

In the Laridae and Alcidae the down barbules are shorter, with indistinct nodes on the proximal portion, and well-developed prongs distally, thus very closely resembling the Colymbiformes.

d) Relationships

The unquestionable likeness of the structure of feathers in the Alcidae to that in the Colymbiformes very strongly suggests the close relationship between them. The relation of the Laridae to the Alcidae, and of the Limicolae to the Laridae, is just as plainly indicated, and we have a very clear and distinct path of evolution suggested by these groups. Relationship to the Gruidae is also suggested and it is probable that the latter represent an early offshoot from the limicoline stem. The Limicolae, in all respects, show higher specialization than the other forms included in the suborder.

e) Summary

The Laro-limicolae are characterized as follows:

(1) Plumules evenly distributed, though sometimes sparse in the Limicolae.

(2) Aftershaft present, sometimes small.

(3) Distal barbules of remiges with broad subnuclear area on base, very small ventral teeth, rather short, subequal hooklets, a series of subequal, somewhat curved ventral cilia, and on inner vane two proximal dorsal cilia more or less earlike.

(4) Proximal barbules with very slender base, inconspicuous ventral teeth, and pennulum little if any over half length of base; proximals of outer vane with imperfectly developed ventral cilia.

(5) Distal barbules of back feathers with a long series of well developed, curved, ventral cilia.

(6) Breast feathers with barbules on outer portion of barbs with flexules.

(7) Down resembling that of Colymbiformes in Laridae and Alcidae, the barbules with enlarged nodes and more or less pigmented in Limicolae.

Suborder PTEROCLO-COLUMBAE

Plate 29

This suborder includes two rather distinct and well-defined groups, the Columbae with the pigeons and doves on the one hand,

and the Pterocles, with the sand-grouse, on the other. The group is characterized by the great reduction of the plumules and the aftershaft. In the Columbæ, which are the most specialized, in this regard, the plumules are entirely absent, and the aftershaft is absent or rudimentary. In the Pterocles, the plumules are evenly distributed, and the aftershaft is present, though small.

a) *Columba livia*

(1) *Remex*

Shaft much deeper than broad at superior umbilicus, for most of length about as broad as wide, with a narrow, median ventral groove, and striations on side, as in *Laro-limicolæ*. *Rami* narrow, the ventral ridge inconspicuous. *Vanules* with very closely set barbules, the distals 45 per millimeter, the proximals about 35.

Inner vane.—*Distal barbules* (pl. 29, fig. 64a) with short wide base, about 0.18 mm. long by 0.037 mm. wide, the ventral teeth very broad and triangular; nuclei in a strikingly diagonal line, even more so than in *Galli*. Pennulum little if any longer than base; more or less arched dorsad; hooklets small and slender, usually 6 in number, proximal 3 short, distal 3 progressively increasing in length; ventral cilia short, curved, subequal, well separated from each other; dorsal cilia straight, spinelike, shorter than ventral ones, the proximal two not especially modified. *Proximal barbules* (pl. 29, fig. 64b) relatively very short and broad, the base about 0.4 mm. long by 0.056 wide, with nuclei in conspicuously diagonal line as in distals. Ventral teeth usually 5, rather narrow and pointed, not elongated, but always evident. Pennulum very slender and filamentous, about half length of base.

Outer vane.—*Distal barbules* (pl. 29, fig. 64c) much like those of inner vane, but, as shown by figure, whole barbule arched dorsad, instead of only the pennulum. Pennulum about as long as base, rather broad in lateral view. Hooklets 6 or 7 in number, small and slender. Ventral cilia as in distal barbules of inner vane, but a little shorter, dorsal cilia developed towards tip, but short and spinelike. Proximal barbules on basal portion of barbs similar to those of inner vane, towards tip ventral teeth become separated from one another, increase in number, sometimes to 7 or 8, and assume a stout curved form, intermediate between typical ventral teeth and typical cilia.

(2) *Other Feathers*

In *Zenaidura macroura*, used as type for description of *back feathers*, latter have distal barbules much like outer vane of remex, and proximals more like inner vane of remex. Distal barbules with short, broad base, broad ventral teeth, and relatively long pennulum, with short, blunt, ventral cilia (pl. 29, fig. 65a). Hooklets characterized by presence of one or two prongs or horns on their distal side, as shown in the greatly magnified hooklet region of a distal barbule from a covert feather of *Columba fasciata* (pl.

29, fig. 67a). Proximal barbules differ from those of remiges in base being relatively slender, with inconspicuous ventral teeth, the pennulum being extremely slender and filamentous, nearly as long as base.

Breast feathers, as exemplified by *Melopelia asiatica*, with both kinds of barbules characterized by elongation of bases, which are relatively more slender than in back feathers, and very great elongation of the slender threadlike pennula. Distal barbules (pl. 29, fig. 66b) have slender base, all barbicels reduced, and pennulum two or three times length of base on more proximal part of vanule, shorter than base on distal part of vanule. Proximal barbules (pl. 29, fig. 66c) with similarly elongated base and extremely long pennulum, several times length of base on proximal part of vanule, about equal to it on distal part.

b) Other Types

In the majority of the Columbidae the *remiges* have a structure very closely similar to that described above for *Columba livia*. A very unusual and probably recent departure from the ordinary type is to be found in the forked primaries of *Drepanoptila*, in which the *entire feather plate is double on the terminal portion*.

Goura coronata differs widely from the other Columbidae in the character of the proximal dorsal cilia of the distal barbules of the inner vane (pl. 29, fig. 70a), which are large and specialized as stout, lobelike projections as in herons and vultures. In other respects the distal barbules, and in all respects the proximal barbules, resemble those of typical Columbidae. The coverts, scapulars, and back feathers undergo very little modification in the different genera except for production of color. (See plate 29, figure 66a, covert from *Melopelia*; figure 68a, covert from *Macropygia*; figure 69a, covert from *Osmotreron*). The *breast feathers* also differ but slightly in different groups. Even in *Goura coronata*, which has feathers differing most widely from the type of any species in the family, the breast feathers are remarkably similar to those of other columbids (pl. 29, figs. 70c, 70d). The barbules on the loose-vaned crown feathers of *Goura* (pl. 29, fig. 70e) have lost their pennula and the bases are cigar-shaped.

In the Pteroclididae, exemplified by *Pteroclis arenarius*, the distal and proximal barbules of the inner vane (pl. 29, fig. 71a, 71c) are distinctly of typical columbid type, but those of the outer vane differ in having very short pennular cells with long, slender ventral cilia and very short, knoblike dorsal cilia. The scapular feathers have the peculiarities of the pennulum of the distal barbules still

more emphasized, the cells being exceedingly short, the crowded ventral cilia being long and slender, the dorsal ones in close juxtaposition to each other, and of a peculiar blunt, heavy form (pl. 29, fig. 71b). The proximal barbules (pl. 29, fig. 71c) are similar to those of the inner vane of the remiges. The barbules of the breast feathers resemble those of the scapulars but are weaker and less perfectly developed.

c) Down

The down barbules of typical Columbæ are long, as in gallinaceous birds, frequently 3 or 4 mm. in length. On the basal part of the pennula there are a number of very large, expanded, and conspicuous nodes, usually from 3 to 8 of them of full size, then a similar number of smaller and less conspicuous ones, decreasing in size until they almost entirely disappear, the whole distal portion of the pennulum being smoothly filamentous or with very minute swollen nodes (pl. 36, fig. 109). Very similar down barbules are found in *Tinamus* and *Nothocercus* among the Crypturiformes.

This structure of down has been found in all species of Columbidae which have been examined except *Goura coronata*. It has been found in *Columba*, *Melopelia*, *Zenaidura*, *Columbigallina*, *Didunculus*, *Macropygia* and *Osmotreron*. In *Goura* the down barbules are shorter than in other Columbidae, not over 2 mm. long, and are smoothly filamentous with the nodes not swollen at all, although the junction of the cells is indicated by the uneven distribution of pigment, the latter being located in the distal portion of the internodes. Nitzsch (1867, pl. 1, fig. 25) figures the basal portion of a down barbule from a turtle dove.

In *Pteroclis* the down barbules are between 1 and 2 mm. long, very slender and delicate, with no indications whatever of nodes, except towards the tip where rather large prongs are developed.

d) Color Modifications

There are a number of special color modifications in the Columbidae which are worthy of special mention. The blue-grays, ranging from light pearl gray in the breast of *Melopelia asiatica* to a slate blue in *Goura*, are very common in birds of this group, as in the Laridae, and are produced in the same way, namely, by a segregation of the black pigment into transverse bars (pl. 29, figs. 64c, 66a-c, and 70c-e) the lighter colors produced by barbules with

wider light interspaces, as for instance, in the breast of *Goura* (pl. 29, fig. 66b-c). It is very unusual, in parti-colored barbules, for any pigment to be present ventral to the row of nuclei. A beautiful, delicate olive color is produced in the coverts of *Osmotreron* by distal barbules in which the base is bluish gray, due to cross-bars of black pigment, while the entire pennulum contains a deep lemon-yellow pigment (pl. 29, fig. 69a). The iridescent neck feathers of *Columba*, *Zenaidura*, and other genera are produced by barbules from which the pennula are broken off, the reflecting surface being the large recurved flange. The barbule drawn on plate 29, figure 57b, from a neck feather of *Columba fasciata* is seen in side view, and nothing of this portion except the tips of the ventral teeth shows as the barbules lie in the vanule, the result being that these feathers are not iridescent on the ventral side (see also Strong 1903b).

e) Relationships

The Pteroclo-columbae, according to their feather structure, show more similarities to the gallinaceous birds than to any other group. The shape of both distal and proximal barbules, and the specialized nature of the down, are all points of striking likeness. The occurrence in the tinamous, which are undoubtedly a specialized group of gallinaceous birds, of both the columbid and galline type of down, might be considered a further bond of union between the two latter groups. They show the same affiliation to some of the gruiform birds as do the gallinaceous birds, and like the latter show some affinity to the Cuculiformes, especially in the presence of prongs on the hooklets of the distal barbules of back and breast feathers. The relation of the Pteroclo-columbae to the Laro-limicolae, if there is any close relationship, is not shown at all in the structure of the feathers. The Pterocles show a number of differences from the Columbae in feather structure, which are probably specializations of their own, and do not show closer approximation to any other group.

f) Summary

- (1) Plumules sparse or absent.
- (2) Aftershaft rudimentary or absent.
- (3) Distal barbules of remiges with short, broad base, nuclei in strikingly diagonal line, ventral teeth broad and triangular; pen-

nulum with 5 or 6 rather small hooklets, a series of short, curved ventral cilia, more slender in *Pteroclis*, and in the inner vane a series of small, spinelike dorsal cilia, the proximal ones of which are especially modified only in *Goura*.

(4) Proximal barbules of inner vane of remiges with short, stout base, moderate, pointed ventral teeth, and very slender pennulum, shorter than base.

(5) Proximals of outer vane, towards tip of shaft, with ventral teeth becoming somewhat cilia-like in form, but a well-formed series of ventral cilia never developed.

(6) Structure of coverts, scapulars, and back feathers much like that of outer vane of remex, except that hooklets of distal barbules frequently have prongs or spines on the edge nearer the tip of the barbule; *Pteroclis* differs in having distal barbules of scapulars with more specialized barbicels than in remex.

(7) Breast feathers with similar structure, but pennula very elongated, no flexules ever developed.

(8) Down barbules in *Pteroclis* and *Goura* moderately long, without enlarged nodes; in all other species examined, the nodes on proximal part of pennula very much swollen and expanded, and very conspicuous, terminal portion of barb smoothly filamentous, or with very minute prongs.

11. Order CUCULIFORMES

This order, composed of two suborders, the Cuculi, including the cuckoos and plaitain-eaters, and the Psittaci, including the parrots, forms a sort of connecting link between the ground birds on the one hand, and the coraciiform and passerine birds on the other. Though the cuckoos and parrots are undoubtedly related, their being grouped together in a separate order has been open to considerable question. In the Cuculi the plumules are very sparse, and restricted to the apteria, and the aftershaft is absent or rudimentary in the Cuculidae, present in the Musophagidae; in the Psittaci the plumules are well developed over the whole body, and the aftershaft is large, but with a short shaft and no distinct vanes.

a) *Coccyzus americanus*

(1) *Remex*

Calamus very small, and of smaller caliber than shaft. *Shaft* at least as wide as deep at superior umbilicus, the widest part of

quill being a short distance distad of this point; ventral groove practically absent; striations on sides at junction of barbs distinct. Pith of *ramus* only one cell in thickness, the ventral ridge relatively wide, its ventral edge smooth in barbs of both vanes. *Vanules* rather open, the barbules set about 28 per millimeter on both distal and proximal ones, although both are composed of rather narrow barbules.

Inner vane.—*Distal barbules* (pl. 30, fig. 72a) with relatively very long and narrow base, about 0.28 by 0.035 mm., the ventral contour sinuate, i. e., broad on proximal half, then becoming narrower in an even curve just proximal to the ventral teeth, which curve slightly outward again; flange very well developed; ventral teeth very small and slender. Pennulum a little shorter than base, all its cells, including those bearing hooklets, not short or crowded together; the hooklets, about 5 in number, small, very frequently with prongs as in *Columbae*, and hanging straight ventrally, i. e., not curved forward as when hooklet cells are crowded; ventral cilia short and appressed to pennulum, the dorsal cilia more prominent, proximal two large and lobate, more distal ones short and spinelike. *Proximal barbules* (pl. 30, fig. 72b) short and slender relative to distals; base about 0.4 by 0.035 mm., ventral teeth short, blunt, inconspicuous, pennulum somewhat shorter than base and rather stout, sometimes with minute, rudimentary barbicels.

Outer Vane.—*Distal barbules* (pl. 30, fig. 72c) with shorter and relatively broader and less sinuate base than those of inner vane; hooklets 5 or 6 in number, cilia as in distal barbules of inner vane except absence of proximal dorsal ones. Proximal barbules on basal half or more of barbs like those of inner vane, on more distal part with a well-developed series of rather short cilia, middle ones of which are hooked (pl. 30, fig. 72d).

(2) Other Feathers

Back feathers with distal barbules much like those of outer vane of remex except that their bases are much more slender, about 0.28 by 0.025 mm., the hooklets usually 4 in number, small, but progressively increasing in length more than in remex, and frequently with prongs; cilia small. Proximal barbules even more slender than in remex, the base about 0.4 by 0.28 mm. Ventral teeth 2 or 3 in number, very inconspicuous, pennulum shorter than base.

Breast feathers almost exactly same as back feathers in structure, but barbules weaker and still more slender (pl. 30, figs. 72e, f).

b) Other Types

The structure of the feathers of all the *Cuculidae* are very similar to the type described as far as examined (*Coccyzus*, *Cuculus*, *Geococcyx*, and *Eudynamis*), except where there are modifications for color production.

The *Musophagidae* do not differ in any important ways from the

Cuculidae in the structure of their feathers, although, as will be shown later, they have a peculiar pigmentation.

The Psittaci differ from the Cuculi to a very slight degree. The barbules of the remiges, as exemplified by *Cacatua galerita* (pl. 30, figs. 74a-d), differ in no important details except the character of the proximal barbules of the distal part of the outer vane, where, instead of the pennulum being long with well-developed hooked cilia as in *Coccyzus* (pl. 30, fig. 72d), the base is shortened, the pennulum also short, and the ventral teeth somewhat increased in number, separated, and in the form of short, more or less triangular barbicels (pl. 30, fig. 74d).

Melopsittacus differs in having distal barbules of the outer vane (pl. 30, fig. 75a) with rather stout bases and short pennula with crowded cells, the hooklets being long and closely approximated to one another and the ventral cilia also rather crowded. The proximal barbules undergo the same sort of modification on the outer part of the barb as in *Cacatua* (pl. 30, fig. 75b).

The body feathers of the Psittaci resemble those of the Cuculi, but differ in that the barbicels are all less highly developed (pl. 30, figs. 76a, 77a, 77b). In breast feathers, frequently, practically all the barbicels are rudimentary or absent, except two or three rather conspicuous hooklets on the distal barbules (pl. 30, figs. 77a, 77b).

c) Down

The down in *Coccyzus*, *Cuculus*, and *Eudynamis* resembles that of the typical Columbidae rather closely, but can readily be distinguished. The barbules are long (2 mm. more or less) and very slender, and the nodes are in the form of round droplets somewhat resembling the viscid droplets on a spider's thread. Those near the base are large, while more distally they are very minute, but still maintain their globular form. In pigmented barbules the pigment is localized in a spot just back of the globular node. The internodes are exceedingly long and slender, in *Eudynamis honorata* sometimes 0.1 mm. long and less than 0.002 mm. in diameter. In *Geococcyx* the globular nodes are not in evidence, the cells being merely gradually enlarged, and pigmented on their distal half.

The down of the Psittaci very closely resembles that of the typical cuckoos, having more or less globular nodes which are rather large

proximally, but very minute distally. In the aftershaft the nodes are not quite so globular, and show rudiments of prongs. In the majority of the Psittaci, the nodes are shaped more like the fruit of a eucalyptus tree, and have the pigment in them instead of proximal to them, thus closely approaching some of the coraciiform birds. The nodes in the Psittaci are somewhat closer together than in the Cuculi, there being usually 15 or more per millimeter, instead of 10 or 12 as in the Cuculi.

d) Color Modifications

There are a number of interesting color modifications in this order. The steel-blue feathers of *Eudynamis honorata* have a warm brown pigment, and are highly reflective, the blue color being probably due, at least in part, to the selective transmission and reflection of the pigment. There are raised ridges at the junction of the cells of the bases of both distal and proximal barbules, and also on the broad pennula of the latter. A similar modification is to be found in the glossy green feathers of *Geococcyx californianus*. In this case the green color seems to be primarily produced by the reflective bases of the distal barbules, but the pennula of the proximals are conspicuously broadened, with distinct raised ridges at the junction of the cells (pl. 30, fig. 73a).

In the Musophagidae, represented by *Turacus corythaix*, the barbules of the remiges owe their deep purplish crimson color to an evenly distributed pigment known as turacin, which, according to Church (1893), is somewhat soluble in water and contains a considerable percent of copper. By transmitted light this pigment in thin layers, e. g., in a single barbule, is of a distinct green color, but in thicker layers, as where the flange overlaps the rest of the base, or where two barbules lie on top of each other, it is a deep red. It is, therefore, a fluorescent color, with color properties somewhat similar to those of eosin. The dull glossy green and delicately lined feathers of the back are produced by barbs in which the barbules are evenly pigmented with a brownish color and are green by refraction, while the rami are whitish.

In the Psittaci a number of interesting color modifications are found. Yellows, reds, and oranges are produced by a pigment evenly distributed in both rami and barbules. Green, blue, and purple are produced by a refraction from the dorsal ridges of the rami, modified by pigmentation in the barbules, e. g., the soft deep

green of many species is produced by a brilliant green structural color in the ramus, accompanied by a brown pigmentation in the barbules, the depth and tone of the green varying with the shade and amount of brown pigment in the barbules. The bright emerald green of *Melopsittacus* is produced by green or blue rami, with lemon-yellow barbules, and the yellow olive-green of *Tanygnathus lucionensis* by green rami and barred barbules which are yellowish proximally (pl. 30, fig. 76a). The deep purple or blue of some species is produced by a brilliant purple or blue structural color in the rami, and a dark brown pigment color in the barbules. One of the most interesting combinations is in the feathers on the side of the head of *Palaeornis cyanocephalus*, which are described as rosy, with a bloom like that of a ripe plum. This is produced by a light purplish blue structural color in the rami, and a red pigment color in the barbules.

e) Relationships

In all respects of feather structure, the Cuculiformes are very closely related to the Coraciiformes, and should probably be considered as nearly allied to the immediate forerunners of this group. The question of their descent is likewise easy, the only lower groups to which they show affinity being the peristeropode Galli and the Columbæ; in general form of pennaceous barbules they are nearer to the former, but in the structure of the down and in some details of the structure of the pennaceous barbules, e. g., the prongs on the hooklets, they show affiliation with the latter. The Cuculi, especially the Musophagidae, come nearer the gallinaceous and columbid birds, while the parrots are nearer the Coraciiformes in the structure of their feathers.

f) Summary

(1) Plumules evenly distributed in Psittaci, sparse and confined to apteria in Cuculi.

(2) Aftershaft present in Psittaci, rudimentary or absent in Cuculi.

(3) Distal barbules and proximal barbules about equal in number.

(4) Distal barbules with very elongate base with sinuous ventral contour, ventral teeth very small; pennulum shorter than base,

hooklets small, sometimes pronged, ventral cilia short and appressed to barbule in inner vane, proximal dorsal cilia lobate, the others short and spiny.

(5) Proximal barbules small and slender, ventral teeth inconspicuous, pennulum rather stout, and shorter than base; well-developed hooked ventral cilia developed in outer vane in Cuculi, but these rudimentary in Psittaci.

(6) Structure of body feathers mere simplification of that of remiges, the barbicels much reduced:

(7) Down in most Cuculi with small globular nodes, larger towards base of barbules, and pigment proximal to them; Psittaci with nodes shaped like eucalyptus fruit, and pigmented.

12. Order CORACIIFORMES

Plates 31-33

This order includes a large number of diversified birds which may be regarded as forming a more or less natural connecting link between the Cuculiformes and lower birds on the one hand, and the Passeriformes on the other. Although some of the included families are undoubtedly near the line of descent of the latter, others are to be regarded as very specialized offshoots, e. g., the Striges, and the Bucerotidae. The suborders Coraciae, Striges, Caprimulgi, Colii, Trogones, Cypseli and Pici, as given by Knowlton and Ridgeway (1909), are not of equal value. In discussing the structure of the feathers in this order, that of a species of the typical suborder will be described in detail and the other families or groups in which important modifications occur will be taken up in order, regardless of the suborders into which they have been grouped.

Throughout the order the plumules are more or less suppressed; in the Alcedinidae they are dense in the apteria, but sparse in the pterylae; in Striges, Caprimulgi and Cypselidae they are present in the apteria only, while in all other forms they are absent entirely. The aftershaft is even more variable, being absent in some, e. g., *Buceros*, rudimentary in others, e. g., Meropidae, and very well developed in others, e. g. Trogones.

a) *Coracias affinis*

(1) *Remes*

Shaft about as wide as deep; median ventral groove small and inconspicuous, striations on sides at junction of barbs slight. *Rami*

narrow, pith more than a single cell in thickness, the *vanules* placed at a low level on sides, so that rami are as high above as below the attachment of barbules. Ventral ridge narrow and inconspicuous. Distal and proximal vanules with about 30 and 22 barbules per millimeter respectively.

Inner vane.—*Distal barbules* (pl. 31, fig. 78a) short and broad, about 0.25 by 0.05 mm., the ventral contour sinuate, and ventral teeth small and fingerlike. Pennulum about as long as base, but very frequently broken off just distal to hooklets. Hooklets moderately long and slender, progressively increasing in length. Ventral cilia straight, inflexible, and subequal in size, the first two slightly longer and closer together on account of crowding together of cells. Dorsal cilia rudimentary, except proximal 2 or 3, which are enlarged and lobate, especially on more distal portion of barb. Proximal barbules (pl. 31, fig. 78b) relatively large, the base about 0.55 by 0.05 mm.; ventral teeth short, triangular and inconspicuous; pennulum a little shorter than base, and considerably flattened for most of its length.

Outer vane.—*Distal barbules* very similar to those of inner vane, except that dorsal cilia are entirely absent, and hooklets are usually 6 in number. Pennulum has some tendency to break off distal to hooklets. *Proximal barbules* on outer part of barb (pl. 31, fig. 78c), with relatively small, slender base, and long pennulum with a well-developed series of ventral cilia which are strongly hooked and reminiscent of the Galli in their high development.

(2) Other Feathers

Back feathers characterized by long narrow base of distal barbules (0.36 by 0.035 mm.) with small, fingerlike ventral teeth, and reduced barbicels, very much as in the Cuculiformes, the hooklets usually 3 in number, but *not* pronged. Proximal barbules exceedingly slender, the base about 0.55 mm. by 0.03 mm., ventral teeth short and pointed, 4 or 5 in number, pennulum somewhat shorter than base and flattened, but not as much so as in remiges. *Breast feathers* of same type, but barbicels of distal barbules more reduced, the cilia being small and the hooklets only two in number, but frequently pronged. Proximals as in back feathers.

b) Other Types

Momotidae.—Remiges in *Momotus* strikingly similar to *Coracias* in all details of structure, the pennula of the proximal barbules slightly broader and more jagged in outline on account of rudimentary *backward-projecting* barbicels. Body feathers with more reduced barbicels than in *Coracias*, often, especially on outer half of barbs, reduced to mere undifferentiated filaments.

Meropidae.—*Merops viridis* like *Coracias*, but proximal barbules on terminal half of barbs of outer vane more slender, with fewer and less well-developed barbicels.

Alcedinidae.—*Ceryle alcyon* differs considerably from *Coracias* in structure of barbules of remiges. Distals of inner vane have long, slender, and conspicuous ventral cilia, and proximals of same vane have shorter pennula, this being only about one-half length of base. On distal half of barbs of outer vane, proximals (pl. 31, fig. 79a) have very short, stumpy bases, and short pennula, the ventral barbicels exceedingly long and strong, in fact relatively larger and stronger than they have been found in any other birds. Distal barbules of back feathers also have long ventral cilia. Breast feathers unusual in having a series of slender ventral cilia on proximal barbules (pl. 31, fig. 79b).

Upupidae.—*Irrisor viridis* has no dorsal cilia whatever on distal barbules even on inner vane of remiges. Hooklets only 4 in number, slender and well separated, ventral cilia well developed, the distal ones more conspicuous on account of the way they lie (pl. 31, fig. 83a). Distals of outer vane have the latter character even more conspicuous. Proximals of outer part of barbs of outer vane have short reduced base, and relatively long pennulum with a series of short weak unhooked ventral cilia (pl. 31, fig. 83b). *Upupa indica* is very similar to *Irrisor* in structure of feathers.

Bucerotidae.—Barbules of remiges considerably modified from type. In *Hydrocorax mindanensis* distal barbules of inner vane (pl. 31, fig. 82a) with very large base with ventral contour strongly sinuate, and ventral teeth relatively large. Pennulum very broad in lateral view in region of hooklets and of first 2 or 3 cells with cilia. Hooklets 4 or 5 in number, very large and heavy, but not elongate; ventral cilia short, stout and blunt, the proximal ones the longer, but not showing when lateral aspect of base is in view on account of twist in pennulum; the more distal ones, however, are in lateral view, so that pennulum appears club-shaped (see plate 31, figures 82a and c); dorsal cilia rudimentary except basal two, which are large and lobate. Distal barbules of outer vane (pl. 31, figs. 82c, d) very similar, but hooklets usually 6, dorsal cilia absent, and width of hooklet region very great, as shown by plate 19, figure 82d. Proximal barbules very long with relatively slender base, 4 or 5 moderate, pointed ventral teeth, and broad pennulum, about half as long as base with backward-projecting rudimentary barbicels. Proximals of outer vane do not have barbicels even on outer part of barb, as shown by plate 31, fig. 82e.

Anthræoceros and *Lophoceros* agree in important details with

Hydrocorax, but in neither are the barbules as large and heavy. The breast feathers and looser back feathers are of the same type as other coraciiformes, but the barbs are very loose distally, soon giving way to a downy structure.

Striges.—The owls are characterized by remarkable softness of their plumage, which, as already shown by Mascha (1904), is brought about by an even more remarkable modification in structure of barbules.

In *Bubo maximus*, on inner vane of remiges, distal barbules (pl. 32, fig. 84a) have base of typical coraciid type, with sinuate ventral contour and small, slender, ventral teeth, but pennulum excessively elongated, frequently reaching a length of over 2 mm., when the base is only about 0.3 mm., being, therefore, nearly seven times as long. The hooklets, 5 in number, very slender, increasing in length to a remarkable degree from the proximal to the distal ones. As shown by Mascha (1904), the pennulum is flattened dorso-ventrally and furnished with a complete double series of both dorsal and ventral cilia, which, however, are curved in such a way that their tips project laterally (pl. 32, fig. 84a). Both dorsal and ventral cilia slender and flexible, the ventral ones, especially on the proximal portion of the pennulum, longer than dorsal ones, the proximal ones of which are not at all enlarged or modified. The proximal barbules (pl. 32, fig. 84b) have an elongate, narrow base, long, slender ventral teeth which, however, lie in close juxtaposition and so are inconspicuous, and an exceedingly long filamentous pennulum, almost as long as that of the distal barbules.

On the outer vane distal barbules differ in that pennulum is much stouter and considerably shorter, with the dorsal cilia entirely absent. Proximal barbules have very slender base and long filamentous but moderately heavy pennulum with a series of very slender, delicate and inconspicuous ventral cilia. Comblike outer margin of outer vane due to curving back of the rami, with an accompanying shortening and stiffening of the barbules and loss of the interlocking apparatus. Plate 32, figure 84c represents a distal barbule from this region of barb.

Body feathers of owls resemble remiges in great length of barbules. The delicate, semi-transparent character, especially of breast feathers, is due to wide spacing of barbs and barbules, the former set about 15 per centimeter on each side, the latter 8 or 9 and 12 to 15 per millimeter on proximal and distal vanules respectively.

In breast feathers barbules almost downy, the base very poorly developed and barbicels greatly reduced (pl. 32, fig. 85a).

The facial disc of owls is the result of a series of very densely set and closely woven feathers. Barbs set 35 or 40 per centimeter and at a very acute angle with shaft, so that they lie very close together, and barbules set about 32 and 38 per millimeter on proximal and distal vanules respectively. Distal barbules have short, stout, tapering bases and short pennula, the cells of which are short and crowded, so that the long, closely appressed ventral cilia are very much crowded.

Caprimulgi.—In *Chordeiles virginianus* distal barbules of inner vane of remiges resemble those of the Striges in form of their base, ventral teeth, and hooklets. Pennulum, as in the Striges, long, but never over 1 mm.; more slender than in owls, and only first 6 or 8 cilia developed, the long series of conspicuous dorsal and ventral ones absent.

In *Podargus strigoides*, filamentous types of distal barbules of inner vane still longer on distal third of barb, being sometimes almost 1.5 mm. long (pl. 32, fig. 87a). Interesting correlative modification in sigmoid backward curve of barbs to give more room for long overlapping pennula and to produce a softer feather. Distal barbules of outer vane in *Chordeiles* with rather short pennula with a well-developed series of ventral cilia (pl. 32, fig. 86a). Proximal barbules on inner vane, unlike owls, have rather short, stout pennula in *Chordeiles*, but in *Podargus* (pl. 32, fig. 87b) pennula are long. In the outer vane, proximals have a series of ventral cilia the more proximal of which are stout and hooked, the more distal ones slender and flexible (pl. 32, fig. 86b).

Body feathers have long, slender pennula, and weakened barbicels, mere simplifications of the remex type.

Although in the great length of the pennula and resulting softness of the plumage the Caprimulgi resemble the Striges, the details of structure, in so far as they differ in these suborders from that of typical Coraciiformes, are not the same, and it is only reasonable to suppose that the similarities are due to parallel evolution and that there is no closer relationship shown between these two groups than between either of them and other coraciiform groups.

Trogonidae.—*Prionotelus temnurus* has structure much like *Coracias*, but especially characterized by form of ventral cilia. Latter very straight and inflexible, and conspicuously larger near

tip than near base of pennulum. No dorsal cilia, even on inner vane, and hooklets moderately long, only 3 in number (pl. 31, figs. 80a, 80b). Proximal barbules of outer vane, on terminal portion of barbs, have ventral teeth increased in number, but remaining blunt, and appressed to barb (pl. 31, fig. 80c), well-developed ventral barbicels never being formed. Body feathers, where not modified for color, with barbules similar to those of remiges, but simpler.

Cypselidae.—In *Cypseloides niger*, on inner vane of remiges, distal barbules have base of typical coraciiform shape, but the ventral tooth, usually single and relatively large, with its tip bent sharply down, giving it a blunt appearance distally. Pennulum with more proximal dorsal cilia developed and stout in form on barbules on outer portion of barbs, on the inner portion only the ventral ones present; these moderate in size and curved as in *Coracias*, pennulum usually breaking off a little distal to hooklets. Proximal barbules with short, broad, tapering bases, the ventral edge more or less scalloped, and pennulum rather heavy, about as long as bases. Body feathers have distal barbules with ventral tooth larger at tip than at base as in some passerine birds. *Chaetura* differs in having broader bases of the distal barbules and rather reduced hooklets.

Trochilidae.—In remex of *Selasphorus rufus*, distal barbules are characterized by disproportionate size of base and relatively large ventral teeth. Proportionate to the size of the base, the hooklet region of the pennulum and hooklets are exceedingly small (pl. 32, figs. 88a and b). In all feathers examined of this species and of several other species the pennulum was broken off one or two cells beyond the hooklets as shown in the figures. The base measures about 0.18 by 0.025 mm., while the pennulum, up to the point where usually broken off, is only one-fifth as long. The proximal barbules have short, broad, tapering bases, with the ventral edge scalloped, ventral teeth inconspicuous and pennulum stout, about as long as base (pl. 32, fig. 88c).

Body feathers have barbs with approximately equal vanules, the barbules very numerous, about 45 per mm. on each side, with their broad surface exposed, but not in contact on feathers without color modifications. Pennula of barbules of both vanules broad and thin, lying in a vertical plane and turned at such an angle with the base as to be parallel with the ramus (see Beebe, 1906, fig. 27). This

gives appearance resembling that of the fused outer bar of proximal vanules of tinamous, but in present case pennula are merely in close juxtaposition.

Coli.—Unfortunately no feathers of birds of this group have been available for study.

Pici.—This suborder, including the Galbulidae, Capitonidae, Rhamphastidae, and Picidae, seems to be intermediate between Passeriformes and Coraciiformes, the Galbulidae being nearer the Coraciiformes, the other families nearer the Passeriformes. In Galbulidae, exemplified by *Jacamerops grandis*, the distal barbules of inner vane of remiges (pl. 33, fig. 91a) very long and slender, the pennulum relatively small, as in Trochilidae. Distals of outer vane similar to those of *Coracias* (pl. 33, fig. 91b). Proximals of inner vane with very long, narrow base and stout, tapering pennulum about half as long as base; on outer vane a well-developed series of hooked ventral cilia (pl. 33, fig. 91c). In the Bucconinae, represented by *Malacoptera fusca*, barbules are of typical passerine type.

In the Picidae the barbules of the remiges are of typical passerine form. Distal barbules of inner vane with relatively large and long base, the subnuclear area suddenly narrowing before the small ventral teeth; pennulum relatively small with all the barbicels well developed, but small (pl. 33, fig. 89a). Proximals of inner vane (pl. 33, fig. 89b) with slender elongate base, inconspicuous ventral teeth, and moderate pennulum somewhat shorter than base. Outer vane differs in distal barbules having shorter base, relatively larger pennulum, and longer hooklets, and proximal barbules having a rather heavy elongated pennulum with short, slightly hooked ventral cilia (pl. 33, figs. 89c and d). The Capitonidae and Rhamphastidae agree very closely with the Picidae, the back feathers of Rhamphastidae, represented by *Rhamphastus ariel*, being reminiscent of the Trogonidae in the straight, inflexible cilia of the distal barbules, these being largest near tip of pennulum (pl. 33, fig. 90c).

c) Down

The down barbules of the various groups of Coraciiformes differ to a very considerable degree, but in nearly all cases they are pigmented and the nodes are more or less distinct.

In *Coracias*, *Merops*, *Momotus*, and *Irrisor*, the down barbules are of moderate length, the cells rather long and gradually swell-

ing on the distal two-thirds of their length, this portion being furnished with a dark pigment (pl. 37, fig. 110). The cells vary from about 20 per millimeter in *Coracias affinis* to about 28 in *Momotus*.

In *Halcyon gularis* the cells are very short and relatively stout, often over 30 per millimeter, and nearly twice as large in caliber as in *Momotus*. Only the terminal third of these cells is enlarged and pigmented, thus giving the barbules a very beady appearance. In *Ceryle alcyon* the cells are longer and more slender, thus being intermediate between *Alcyon* and the more typical *Coraciae*.

In *Hydrocorax mindanensis* (Bucerotidae), the down barbules have a very peculiar and unusual appearance, the cells being very short and thick, as many as 40 per millimeter, with the nodes not enlarged but marked by two sharp, spiny prongs. The pigment is almost uniformly distributed (pl. 37, fig. 111). In *Anthracoceros* the cells are longer and the pigment is confined to the middle of the internodes. The nodes are often very indistinct.

In the Striges the down is very similar to that of the Cuculiformes. In *Bubo maximus* the barbules have three large nodes on the inner part of the pennulum, shaped more or less like the fruit of a eucalyptus tree. Following these the cells are of the type found in *Coracias* but very elongate, 9 or 10 per millimeter, with the pigment confined to the distal one-fourth or one-fifth. In *Aluco pratincola* the structure is similar, but there are usually five instead of three enlarged basal nodes, and sometimes a few globular, droplet-like nodes as in *Coccyzus*.

In the Caprimulgi the nodes are usually rather indistinct, especially in the Caprimulgidae, where they are almost imperceptible, although the pigment is restricted to a spot near the distal end of each cell. In *Podargus* the down is like that of *Coracias*.

In *Cypseloides* and *Chaetura*, representing the family Cypselidae, the down barbules are similar to those of the Caprimulgidae, the cells having dark pigment in their distal portions and light pigment in their proximal portions, the nodes being indistinct.

In the Trochilidae the structure of the barbules on the more basal portion of the well-developed downy barb is totally different. The bases of these barbules, unlike those of any other birds except the Passeriformes and Pici, are considerably enlarged and widened on the barbules near the base of the barbs, and have irregular villi on the ventral side, as shown in plate 37, figures 112*a* and *b*. The pennula are furnished with large, conspicuous nodes of a peculiar

type for their entire length, and have short internodes (pl. 37, fig. 112). The down barbules of a large number of genera of Trochilidae have been examined, and all of them have been found to possess this type of structure. The barbules on the outer part of the barbs have inconspicuous nodes, of a type similar to that shown in plate 37, figure 110.

The Trogons have down very much like the Trochilidae in that the nodes are large and conspicuous and present for the entire length of the pennula, but they are not relatively as large, or the internodes as short, and the bases are not furnished with villi. The nodes are shaped more or less like the fruit of a eucalyptus tree and are deeply pigmented.

The down barbules of the Pici, like the pennaceous barbules, show a close similarity to the Passeriformes except in the family Galbulidae. In the latter, as exemplified by *Bucco*, *Malacoptera* and *Jacamerops*, the down is like that of *Coracias* and *Momotus*. In the Rhamphastidae (*Rhamphastus*, *Pteroglossus* and *Andigena*) the barbules (pl. 37, fig. 113) have large nodes shaped like eucalyptus fruits on the proximal portion, these becoming small and insignificant beyond the basal 6 or 7. The bases of the inner barbules have weakly developed villi. The barbets, Capitonidae, have down almost exactly like the Rhamphastidae. In the Picidae the type is similar except that the basal nodes are relatively smaller, and the decrease in size toward the tip of the barbules is more gradual and less conspicuous. The villi on the bases are well-developed on the barbules near the base of the barbs, as much so as in many Passeriformes.

d) Color Modifications

The variety of colors found in the Coraciiformes is unexcelled anywhere amongst birds, and the variety of structural modifications correlated with color production is correspondingly great.

Many of the Coraciiformes are characterized by the prevalence of deep purple and light blue colors in the wings and tail. The deep purple is a brilliant purple refraction color produced by the large dorsal ridges of the rami, combined with a blackish brown pigmentation in the non-refractive barbules. The beautiful light blue of these birds is produced by a superstructure above the refrangant surface of the dorsal ridges of the rami which otherwise produce brilliant purple, the barbules in this case being unpig-

mented and almost transparent. Gentle scraping or light pressure destroys the superstructure of the rami, leaving the purple hue, while crushing destroys this color also and the barb appears blackish. The beautiful light blues and purples of the Old World kingfishers and rollers are produced in this way.

Dull or olive-green, as in the back and breast of species of *Merops* and *Momotus*, is always the result of structural color in the rami and black or brown pigment color in the barbules, while bright, metallic, or iridescent greens, such as that of the back of *Jacamerops*, the breast and plumes of many trogons, the breast of *Irrisor*, and of many other species, are the result of refraction from the barbules. In *Jacamerops* and *Irrisor* it is produced by the slightly modified bases of the barbules. In the trogons the brilliant green is produced by barbules which are entirely metamorphosed into color-producing structures which are non-coherent and do not lie flat, the result being the beautiful effect of tinsel so characteristic of these birds (pl. 31, fig. 81a).

The blue-gray of *Ceryle alcyon* is produced, as is that of the gulls, by irregular distribution of black pigment (pl. 31, fig. 79a). Blue, like green, is produced either by refraction from the rami accompanied by light or dark pigment color in the barbules, or by refraction from the latter.

The brilliant iridescent gorget feathers of hummingbirds are among the most interesting color-producing structures to be found. In this case the color is produced by barbules the flanges of which are very broad and recurved, being in some cases wider than the portion of the feather not turned over (pl. 32, fig. 88d). These barbules, like those of the back and breast feathers which are not modified for the production of color, have broad pennula which lie in a line on the outer edge of the vanule, parallel with the ramus, and are unpigmented, and therefore inconspicuous. In the iridescent color-producing feathers, the bases of the barbules are so broadened as to produce a solid vanule, i. e., without spaces between the barbules. In the green and blue colors of *Petasophora anais*, the refraction is from the portion of the barbules which is not curved over, while in the brighter green of *Eugenes fulgens*, and in all lilac, ruby, or fiery red colors, it is from the broad, recurved flange (pl. 32, fig. 88d), the latter being also produced medially in order to cover the ramus and meet its fellow from the opposite side.

In hummingbirds alone are there to be found red, lilac, or ruby

colors which are due entirely to refraction, the pigment being of a totally different color. It is interesting to note that in blue iridescent feathers the underlying pigment is a rich rufous brown, in green a duller fuscous brown, and in all shades of red a very dark olive-green, brighter in the fiery red of *Selasphorus rufus* than in the lilac or ruby red of other species. This phenomenon is explained by the theory of selective transmission and reflection, colors which are readily reflected being poorly transmitted.

In various other types of coraciiform birds still other interesting color modifications are to be found, only a few of which may be mentioned here. The coppery green of *Jacamerops grandis* is produced by barbules very similar in form to those of hummingbirds, the color being reflected from the portion of the barbule not curved over, as in *Petasophora*. Green in the Capitonidae is produced in an interesting manner, the portion of the ramus ventral to the attachment of the barbules having a deep yellow pigment color, while dorsal to the barbules the rami are curved over flangelike, contain a rich brown pigment, and produce a blue structural color. The combination of blue and yellow by reflected light gives the effect of green, while by transmitted light it is orange brown. The depth and tone of the color varies with the pigment in the non-refrangent barbules. In the woodpeckers the red crests which are so frequently found owe their color to prolonged, cylindrical rami which are filled with a deep red pigment. The peculiar effect of the white and red streaked breast of *Asyndesmus torquatus* is due to a deep red pigmentation in the dorsal half of the rami, and a white effect in the ventral half, appearing under the microscope like a miniature snow bank, due to the countless minute air spaces which cause diffusion of light.

e) Relationships

The Coraciiformes, as stated at the beginning of the discussion of them, constitute a rather heterogeneous assemblage of birds which lie between the Cuculiformes and the lower orders on the one hand, and the Passeriformes on the other. The Coraciidae and near allies, Striges, Caprimulgi, Bucerotidae and Cypselidae, have types of feathers which are to be regarded as independent offshoots from the main line of evolution. The trogons seem to be more nearly in the line of descent of the passerine birds, the Rhamphastidae and Capitonidae of the suborder Pici connecting them with the latter

group. The Trochilidae and the suborder Pici, with the exception of the Galbulidae, show such striking likenesses to the Passeriformes that it is difficult to deny their closer alliance to that group than to the Coraciiformes.

f) Summary

The Coraciiformes are characterized as follows:

(1) Plumules more or less suppressed, or confined to apteria.
(2) Aftershaft variable, being absent, rudimentary or well developed.

(3) Distal barbules of remiges with bases different in different groups but always with small slender ventral teeth; pennulum moderate, with usually not over 5 hooklets, the ventral cilia moderate, straight, usually longer and more conspicuous near tip of pennulum than at its base; dorsal cilia as a rule poorly developed. Exceptions in the relatively stout, blunt ventral teeth of Trochilidae, the extremely long pennula of Striges and Caprimulgi, and the minute pennula of Trochilidae, the poorly developed ventral cilia in the inner vane of *Podargus*, in the large number of stout hooklets in the outer vane of Bucerotidae, and in the relatively high development of the proximal two dorsal cilia in the Bucerotidae.

(4) Proximal barbules of inner vane of remiges usually with slender elongate base, moderate ventral teeth, and rather broad pennulum somewhat shorter than base. Exceptions in short broad bases in Trochilidae, and in greatly elongated pennula in Striges and Caprimulgi.

(5) Proximal barbules on distal part of barbs of outer vane of remiges with moderately developed series of hooked ventral cilia. Exceptions in enormous talon-like ventral cilia of *Ceryle*, non-barbicelled pennulum of Bucerotidae and Trochilidae, and weak cilia of trogons, hoopoes and owls.

(6) Body feathers, where unmodified for color production, mere simplifications of remex type.

(7) Down always more or less pigmented, with nodes slightly enlarged and inconspicuous in typical coraciid forms, larger and beadlike in Alcedinidae, and almost unnoticeable in Caprimulgi and Cypselidae; barbules coarse, with prongs at nodes, in Bucerotidae; nodes large basally and inconspicuous distally in Striges and

Pici; bases of down barbules with villi on ventral edge in Trochilidae and Pici (except Galbulidae).

13. Order PASSERIFORMES

Although containing nearly one-half of all known birds, this order forms a very compact group, all the members of which are so closely related that the entire order is hardly more diverse in its forms than is a single suborder in other groups, and although they are divided into numerous families, these have hardly more than generic or supergeneric value as compared with families in most other groups. As would be expected, the feather structure varies but little in the different forms, in this regard the Passeriformes being in sharp contrast to the Coraciiformes.

In all of the Passeriformes the plumules are very sparse in the apteria, or are absent entirely. The aftershaft, though sometimes rudimentary or absent, is usually present, being composed of a few long, straggly barbs, and a very short shaft.

a) *Cyanocitta stelleri*

(1) Remex

Shaft about as broad as deep, the median groove small and inconspicuous, striations on sides at junction of barbs inconspicuous or absent. Pith of *rami* only a single cell thick, the *vanules* set low, ventral ridge well developed, with smooth ventral edge. Vanules each with about same number of barbules, about 28 in each.

Inner vane.—*Distal barbules* (pl. 33, fig. 92a) of same type as in *Melanerpes formicivorus* (compare plate 33, figure 89a with plate 33, figure 92a). Base very large and elongate, about 0.35 by 0.035 mm., the broad, filmlike, subnuclear area curving in just proximal to ventral teeth, so that at this point the base is very narrow; ventral teeth small and slender. Pennulum relatively very small, less than half length of base; hooklets 3 or 4 in number, small, subequal, and never with prongs; ventral cilia small, more or less appressed to pennulum, and inconspicuous; dorsal cilia short and spinelike, the basal two somewhat enlarged, but not lobate. *Proximal barbules* (pl. 33, fig. 92b) with base relatively small compared with that of distals, about 0.37 mm. by 0.035 mm., the ventral edge scalloped more or less, ventral teeth short, pointed, and inconspicuous; pennulum moderately flattened, about two-thirds as long as base.

Outer vane.—*Distal barbules* (pl. 33, fig. 92c) with much shorter and broader base than in inner vane, about 0.22 mm. by 0.04 mm., the broad subnuclear area as in the inner vane but curved more conspicuously towards next succeeding barbule. Pennulum relatively longer, hooklets similar, ventral teeth better developed, larger distally on barbule, as in trogons and Pici. *Proximal barbules*

(pl. 33, fig. 92*d*) similar to those of inner vane, the bases becoming shorter on distal third of barbs. At extreme tip, base reduced and almost lost, the pennulum weak, with small barbicels on both dorsal and ventral sides.

(2) Other Feathers

Plumage of *back* and *breast* rather hairlike, due to non-coherence of barbs on their outer portions, on account of very loose interlocking of barbules. Vanules open, i. e., with wide spaces between barbules, due to vertical position of latter and to their wide spacing, there being only about 18 or 20 per millimeter on each side. Distal barbules (pl. 33, fig. 92*e*) with narrow tapering bases which have ventral part curved slightly toward next succeeding barbule, as in remiges; barbicels all greatly reduced or missing, except 2 slender but persistent hooklets. Proximal barbules (pl. 33, fig. 92*f*) with no sharp demarcation of base and pennulum, except a bend; form narrow, and tapering from slightly expanded proximal portion of base all the way to tip; total length about 0.8 mm.

b) Other Types

Throughout the group, except in case of color modifications, there is very little divergence from this type. In *Corvus corax* the ventral teeth of the distal barbules are more highly developed than usual, being rather broad and triangular, and sometimes bifurcated at the tip; in this species, also, the two basal dorsal cilia reach an unusually high degree of development, as in the case of *Hydrocorax* among the Coraciiformes. Proximal barbules of outer vane develop ventral cilia only at extreme tip, the ventral teeth in these barbules becoming separated from one another, and assuming a short spinelike form.

In the Frigillidae, Bombycillidae, Icteridae, and other families more or less closely related to the finches, the distal barbules are characterized by the peculiar form of the ventral teeth, which are relatively very long and large, being broader at the middle of their length than at their base. This character is shown in plate 33, figure 94*a*, representing a distal barbule from the inner vane of a remex of *Pipilo maculatus*. In some genera of the Turdidae, e. g., *Planesticus*, there is a tendency for the distal barbules to adhere to each other by means of the greatly elongated ventral teeth which behave as if weakly fused with each other into a longitudinal bar, not unlike the bar formed by the pennula of the proximal barbules in Tinamous.

In the Tyrannidae, and to a greater or less extent in the Mniotiltidae, Vireonidae, Turdidae, and many other allied families,

the proximal barbules on the outer half of the barbs of the outer vane of the wing feathers undergo a rather sudden change. On the inner portion of the barbs, the proximal barbules have moderate bases and unusually broad pennula, but near the middle of the barb the base suddenly becomes greatly reduced and the pennulum elongated, the latter with a series of strong, hooked, ventral cilia which are very conspicuous (pl. 33, fig. 93a). Concomitant with this specialization of the proximal barbules, the distals deteriorate, the differentiation between base and pennulum being lost, the former being short and triangular, only about 0.1 mm. long to the point where it merges into the pennulum; no barbicels except a few rudimentary dorsal and ventral ones near tip.

Although representatives of a very large number of passerine families have been examined, no further modifications worthy of special mention here have been found in the group, except in connection with color production or some other macroscopic effect, as in the ornamental plumes of birds of paradise and lyre birds. Plate 33, figure 95a shows the tip of a "wax-tipped" feather of *Bombycilla garrula*, showing the method of fusion of shaft with outer vane only. This "wax-tip" has usually been looked upon merely as the expanded terminal portion of the shaft.

c) Down

With the exception of its occurrence also in the Trochilidae and all of the Pici except the Galbulidae, the down barbules of passerine birds have a constant and peculiar character in the presence of lobate or fingerlike villi on the ventral edge or on the side of the base, as shown in plate 37, figure 115b, and also in figures 114a and b, and 115a of the same plate. Down from over one hundred species of passerine birds has been examined, these being representatives of as diversified families as could be obtained, and this character has never been found missing on the barbules near the base of the well-developed downy barbs. It is never present, as far as I have observed, on the barbules on the more distal part of the barbs, nor in the aftershaft.

The pennula of the downy barbules are of moderate length, ranging from about 1 mm. in most forms, e. g., *Myiarchus* and *Turdus*, to 5 mm. in *Menura*. With a few exceptions, as in *Haematoderus* (Cotingidae), in the red shoulder patches of *Agelaius phoeniceus*, and in a few other cases, usually where the feathers are red,

the down is pigmented, and grayish in color. The nodes, except in such unpigmented down as that referred to above, are always conspicuous, but not strikingly larger near the base of the barbule than at its tip. The shape of the nodes and length of internodes varies considerably in different birds, the nodes being shaped like a eucalyptus fruit in *Corvus* (pl. 37, fig. 115), and spaced about 22 per millimeter; of similar shape, but about 32 per millimeter in *Myiarchus*; more rounded and about the same number in *Menura*; of *Coracias* type (pl. 37, fig. 110) in *Cinclus*; exceedingly numerous and prominent in the Mniotiltidae, 35 or more per millimeter, and even more numerous in some of the Fringillidae (pl. 37, fig. 114).

d) Color Modifications

The colors of passerine birds are produced in much the same way as in the Coraciiformes. Yellow is produced either by structure, pigment, or both. The yellowish straw color of the head and neck feathers of *Paradisea apoda* is due almost if not entirely to structure; the yellow of the belly feathers of *Myiarchus cinerascens* and *Tyrannus verticalis* to a combination of a structural modification and an underlying yellow pigment; the yellows and orange yellows of *Oriolus* and various species of Mniotiltidae to pigment only, distributed in both rami and barbules.

Red, as far as I have observed, is always the result of pigment, frequently deepened in color by the high polish of the barbs in which it occurs. Dull reds, such as that on the breast of *Piranga rubra* are produced by pigment on both rami and barbules. The fiery red crests of *Tyrannus* and *Pyrocephalus* are produced by red pigment in naked rami which have diagonal lines running partly across them, these representing rudimentary barbules arrested in their development, and fused with the ramus. Other deep and intense reds are produced by naked barbs which sometimes have no structural modifications.

The deep blue of *Progne subis* is due to barbules which are reduced to straight flattened bands partially overlapping each other, and with refrangent surfaces, the tips always broken off, leaving the ends truncate. The bright blue of the lazuli bunting, *Passerina amoena*, is produced by refraction from naked rami.

The brilliant red and green feathers of *Nectarinia famosa* are worthy of special mention. The tips of the rami in these feathers are naked and have a deep red color, thus giving the shining red

edges to the feathers. The inner portion of the barbs has no red in the rami, and has a series of closely-set flattened barbules, resembling the pennula in green speculum feathers of ducks in that there are constrictions between the cells, and each individual cell is more or less warped and spoon-shaped (Gadow, 1882, pl. 28, figs. 9a, b). These barbules produce a brilliant green refraction color, and thus give the green color to the inner portion of the feather. The minute details of the method of refrangent color production in pittas has been worked out by Gadow (1882), and Strong (1902).

e) Relationships

The Passeriformes, according to feather structure, are to be regarded as a compact group in which, in spite of the large number of species, very little divergence has taken place. It constitutes a terminal branch of the phylogenetic tree, its next lower relatives being undoubtedly the Coraciiformes, especially the suborder Pici, which, however, is probably to be regarded itself as a member of this group rather than of the Coraciiformes.

f) Summary

The Passeriformes are characterized as follows:

- (1) Plumules sparse in apteria or absent entirely.
- (2) Aftershaft absent, rudimentary, or in the form of a few long, straggly barbs.
- (3) Distal and proximal vanules of remiges with about equal number of barbules.
- (4) Distal barbules of remiges very large relative to proximal barbules, the bases of each type about equal.
- (5) Distal barbules of inner vane of remiges with large elongate base, with broad filmlike subnuclear area not extending all the way to ventral teeth; ventral teeth small and slender, as in Coraciiformes, or elongate and enlarged distally; pennulum relatively small, the hooklets moderate and well spaced, ventral cilia short, and subequal, dorsal cilia small, the basal two more or less enlarged.
- (6) Distal barbules of outer vane of remiges with much shorter base, and relatively larger pennulum and hooklets.
- (7) Proximal barbules of inner vane of remiges with elongate, relatively small base, inconspicuous ventral teeth, and pennulum shorter than base.

(8) Proximal barbules of outer vane of remiges without ventral cilia except at extreme tip of barbs, or with a sudden transition at about middle of barb.

(9) Looser body feathers with barbules very much reduced and simplified, with all barbicels rudimentary or absent except two or three hooklets on distals.

(10) Down barbules with lobate or fingerlike villi on base, the pennulum with more or less distinct nodes, the latter not strikingly larger near base of barbules.

IV GENERAL CONCLUSIONS

1. *Taxonomic Value of the Structure of Feathers*

The systematic study of the structure of feathers of different groups of birds which has been made and presented in the preceding pages cannot but impress one with the fact that the morphology of feathers, in other words, the epiphylogy of birds, is as valuable from a taxonomic point of view as is osteology, myology, or the systematic morphology of any other organ or system of organs of the body. Not only is the difference between birds of different groups of larger content as clearly marked in the structure of their feathers as in the structure of any other system of organs, but the fact that most of the modifications in these minute details of structure which are found in different groups of birds can be of little or no adaptive value, increases the taxonomic value beyond that possessed by most other organs, since parallel or convergent adaptive evolution is largely eliminated. As in all other organs, parallel evolution which is not necessarily correlated with adaptation may take place, and undoubtedly has done so, with the result that the structure of feathers alone is not a safe criterion of relationship any more than is the structure of the bones or muscles. Taken in conjunction with the evidence furnished by other organs and systems of organs, however, and with these as a general guide, the cases of parallelism in evolution can in most cases be discovered, and the evidences of relationship and phylogenesis furnished by the morphology of feathers is then of the very highest value.

As has been pointed out by Cockrell (1911a), the scales of fishes are unquestionably of great taxonomic value. Work on the

scales of reptiles and on the hair of mammals shows promise of bringing out facts concerning them also, which will be of taxonomic value. But in all of these the range of possible or probable modifiability is very slight as compared with that of feathers, on account of the much greater complexity and minute structural units of the latter, and therefore the morphology of feathers is of greater value than lepidology or any other branch of epiphylogy from a taxonomic point of view.

2. *Principal Modifications of Structure Useful in Taxonomy*

There are a great many different parts of feathers and plumage which show phylogenetic modifications, among which some are of great value and can almost certainly be depended upon to be of importance in showing relationships, while others are as plainly of very doubtful value. From the foregoing systematic study of the different groups of birds, the relative value of the different structures and arrangements of different parts of feathers has made itself apparent, and the following general conclusions may be drawn.

The *distribution of plumules* is a character which, in itself, is of little value, on account of its great variability, in a few cases, within a single group, and on account of the adaptive value of the plumules, as shown by their presence in all the lower orders of water-birds and their recurrence in kingfishers amongst a group in which there is elsewhere a tendency for plumules to be reduced or entirely lost. However, in conjunction with the condition of other structures, the distribution of plumules is of some phylogenetic importance.

The *aftershaft* is of more importance, and its presence or absence, and form if present, may be depended upon to a considerable extent as showing phylogenetic tendencies.

The *quill*, even of the remiges, is too variable within groups to be of any great value except in a few cases, as, for instance, in the Anseres, where the disproportionate length of the calamus is of diagnostic value. The condition of the ventral groove and of the striations on the sides are of little value except in a few cases.

The *rami* have a number of characters which are significant, namely, the thickness of the pithy portion, whether of one or more layers of cells (see Mascha, 1904), the width relative to the shaft, the relative size and form of the ventral ridge, and the presence or absence of villi on its ventral edge in the outer vane.

The *distal barbules* of the remiges have a number of characters

which are of high value from a taxonomic point of view, namely, the number and size relative to the proximal barbules, the form and general character of the base, the general size and form of the pennulum relative to the base, the number, size, shape, and general characters of the various kinds of barbicels, especially the ventral teeth, ventral cilia, and basal dorsal cilia, and finally, the differences between the distal barbules of inner and outer vane.

The *proximal barbules* are far less variable than the distal barbules, and as a rule are of much less taxonomic value. Their chief phylogenetic modifications are in the following: size of base relative to distal barbules, and relation of width to length; number, form, and conspicuousness of ventral teeth; form of pennulum, and length relative to base; and condition of ventral cilia in barbules near the tip of barbs in the outer vane.

The chief value of the *body feathers* lies in the degree and manner of simplification of the barbules from the remex types, and the presence or absence, and form, if present, of flexules.

The *down barbules* from the region of the superior umbilicus of remiges and large coverts, and from the less developed portions of barbs of other feathers, e. g., at the tip of the barb, are not always of taxonomic value, but the typical down barbules from a portion of the feather where they reach their highest development, as for instance near the base of the distal vanule of a well-developed downy barb, are of very great value from a phylogenetic point of view; in fact, it is frequently possible by means of the down alone to identify the group to which a bird belongs and unquestionably to determine its relationship to other groups. The characters which are of value are the length, the size and form of the base (of value only in the case of some Coraciiformes and Passeriformes), the character and frequency of the nodes, and the presence or absence of prongs.

Methods of color production are of more or less taxonomic value in certain cases. For instance, the iridescent colors of ducks and other water-birds are produced differently than in gallinaceous birds, and in both of these differently than in Coraciiform birds.

3. Relationships of Groups Suggested or Corroborated

The morphology of feathers, as presented in the preceding pages, adds one more basis for comparison of different groups of birds, and seems to throw new light on the relationship of certain groups to others. A classification which even comes near to expressing true

relationships cannot be based on any single character; it must be a composite picture of the evidence furnished by *all* the characters.

In the following paragraphs there is given a summary of the evidence furnished by one single small character, the morphology of the minute structure of feathers. In itself it is obviously inadequate. Taken in conjunction with the evidence furnished by other characters, however, it is hoped that the evidences of relationships suggested by epiphylogeny may help to bridge the gaps left by other comparative studies, and so help to complete and perfect the chains of relationship in avian phylogeny.

Beginning with the Ratitae, the structure of the feathers of the various orders included in the group gives very strong evidence in favor of their being primitively rather than secondarily flightless birds, the Struthioniformes and Rheiformes apparently being end branches of one main evolutionary stem, and the Casuariiformes and Apterygiformes similar end branches of another stem which is probably to be considered a little nearer to the line leading to the Carinatae (see summaries on pages 288, 290, 293, 295).

Among carinate birds the most primitive feathers are to be found among the penguins, and next above them the Colymbiformes (for details, see pages 298 and 302). From this group two important lines of evolution are suggested, one leading up through the Alcidae to the Laridae and Limicolae, and through the Rallidae and Gruidae to the Galli, Columbidae, and finally the Passeriformes, while the other leads through the Procellariiformes and Ciconiiformes to the Anseres and Falconiformes. While the writer does not believe that this is necessarily the true phylogenetic relationships of the various groups, nor even contend that it is *nearly* the correct interpretation, nevertheless with the facts now at hand, it satisfies the conditions of the feather morphology better than any other interpretation at present available. According to morphology of feathers there is strong evidence for the following hypotheses:

(1) The Procellariiformes, while constituting a specialized offshoot, lie near the line of descent of the Ciconiiformes, the nearest of the latter order to the primitive type being the Steganopodes, while the Ardeae are the most specialized.

(2) *Plotus* and *Phalacrocorax* deserve to be separated into two distinct families, the former showing remarkable likenesses to the Cathartae.

(3) The Phoenicopteri have a type of feather structure which is intermediate between that of the Ciconiae and the Anseres (see summaries on pages 320, 326 and 330).

(4) The Phaethontidae seem to be more closely related to the Laridae than to the Steganopodes.

(5) The Alcidae show very striking similarities to the Colymbiformes, and likewise appear to be closely related to the Laridae, and may therefore be considered as more or less intermediate.

(6) The Gruiformes, while having some features in common with the Ciconiiformes, seem to be nearer the Limicolae, this being especially true of the Rallidae and Aramidae.

(7) The strikingly heronlike epiphylogy of *Eurypyga* and *Cariama*, at least of *Eurypyga*, suggests the possibility of their being grouped as aberrant Ardeae.

(8) *Cursorius*, representing the family Glareolidae, appears to be out of place, and to find its nearest affinity with the Ardeae, rather than with the Limicolae.

(9) The Pteroclo-columbae seem more closely related to the gallinaeous birds, especially the alectoropode Galli, than to the Larolimicolae, with which they seem to have no real relation (see summary, page 362).

(10) The Tinamidae show strong evidence of being a highly specialized offshoot from the Galliformes (see summary, page 347).

(11) The Cuculiformes are more or less intermediate between the peristeropode Galliformes and Columbae on the one hand, and the Coraciiformes on the other, but seem not to differ to a sufficient extent from the latter to warrant their separation into a distinct order.

(12) The Trochilidae and all of the suborder Pici, with the exception of the Galbulidae, appear to be more closely related to the Passeriformes than to the Coraciiformes.

(13) The Galbulidae show evidence of not belonging with the Pici.

With the exception of these relatively few cases of disagreement with the phylogenesis and relationships accepted by Knowlton and Ridgway (1909), the evidence of the morphology of feathers strongly supports the grouping made by these authors, this in turn being the grouping made by Gadow (1891), with a few minor modifications.

4. *The Phylogenesis of Birds as Modified by Morphology of Feathers*

As intimated above, distinct lines of evolution in the modification of the structure of feathers are clearly shown by this study. After making a careful analysis of these various lines of divergence, which seem to be more or less orthogenetic in nature, a phylogenetic tree representing the evolution of birds has been worked out, and is presented in fig. G (p. 391). In so far as it is in accord with the facts of morphology of the feathers, the classification presented by Knowlton (1909) has been adhered to in the preparation of this evolutionary tree, since it is believed that this classification is most nearly in accord with the views of most of the leading ornithologists of the present time, and most nearly embodies the evidence furnished by recent work on comparative avian anatomy and morphology. In all cases in which the evidence furnished by morphology of feathers is distinctly not in accord with Knowlton's interpretation of relationship, the classification has been altered so as to agree with the facts of epiphylogeny presented in this paper. The phylogenesis presented, therefore, is one which is based primarily on morphology of feathers, but in which the system presented by Knowlton (1909) has been adhered to in so far as there was no conflict. While it is not supposed that such an interpretation of relationship is necessarily the correct one, or that some other interpretation may not be made which will better satisfy all the conditions of avian structure, it is hoped that the accompanying phylogenetic tree will be of use to taxonomists in the embodiment of the facts presented in this paper in the preparation of a system of classification which will best satisfy the conditions of *all* branches of the comparative morphology of birds.

Transmitted April 17, 1914.

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EXPLANATION OF PLATES

Except as otherwise noted, all figures of barbules are from a typical portion of a typical barb of the feathers it represents, and drawn in lateral view, the distals with their bases to the left, the proximals to the right, and in all cases dorsal side uppermost on the plate.

PLATE 13

RHEIFORMES AND STRUTHIONIFORMES

All figures except 2*d*, $\times 85$

- Fig. 1. *Rhea americana*.
a. Barbule from basal portion of barb from terminal part of remex.
b. Barbule from basal third of barb from middle portion of rump feather.
c. Barbule from middle portion of barb from middle part of remex.
- Fig. 2. *Struthio camelus*.
a. Barbule from remex.
b. Barbule from back feather.
c. Barbule from black wing covert.
d. Elongated barb from back feather of chick (neossoptile). $\times 10$.
e. Barbule from back feather of chick (neossoptile).

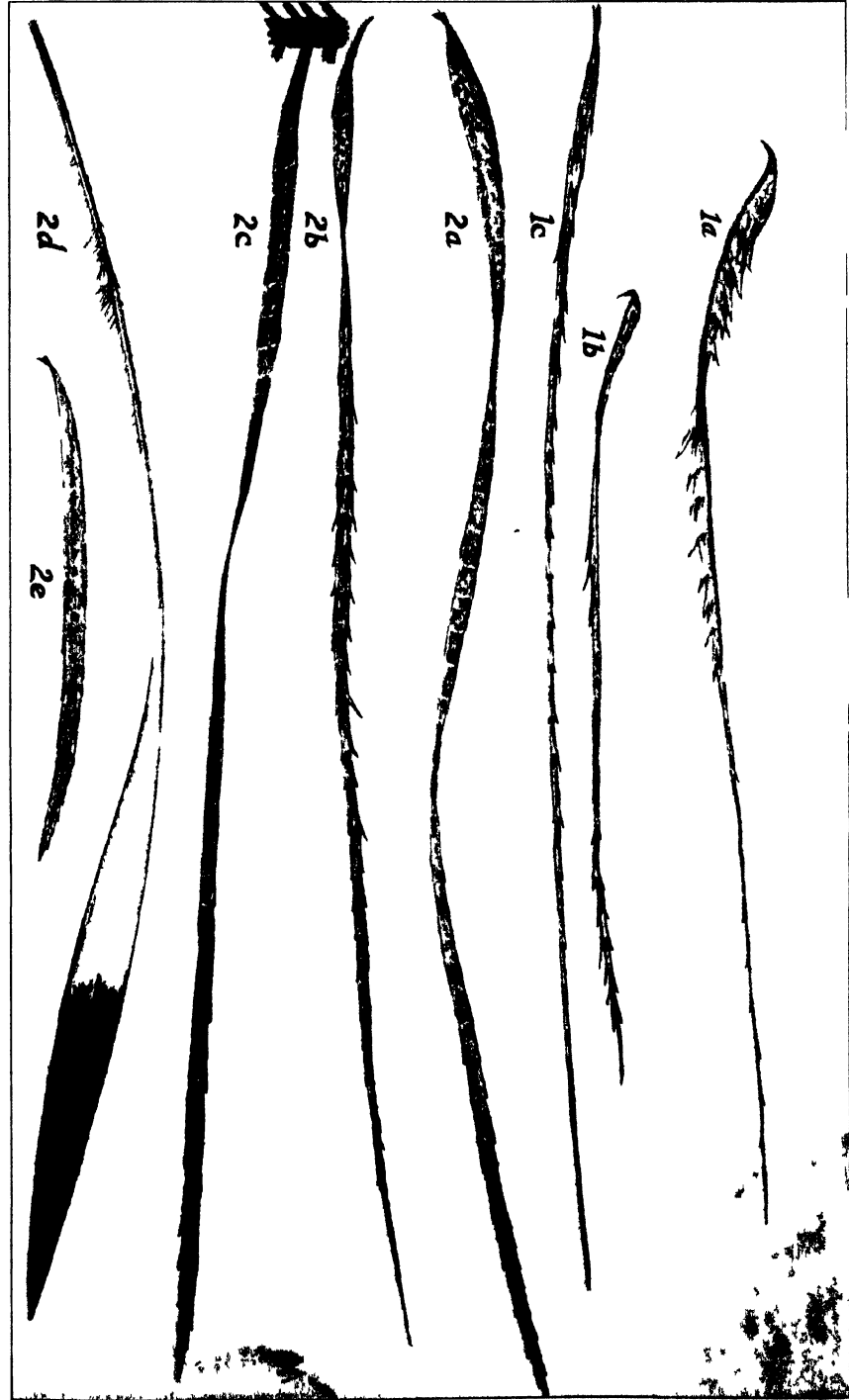


PLATE 14

CASUARIIFORMES AND APTERYGIFORMES

All figures, except 4a and 5b, \times 140

- Fig. 3. *Casuarus papuanus*.
a. Portion of barb from basal portion of contour feather.
b. Tips of barbules from same barb.
- Fig. 4. *Dromaeus novae-hollandiae*.
a. Tip of naked barb from distal part of contour feather. \times 35.
b. Proximal and distal portions of barbule from contour feather.
- Fig. 5. *Apteryx haasti*.
a. Proximal and distal portions of barbule from back feather.
b. Similar barbule. \times 85.



PLATE 15

SPHENISCIFORMES

Figs. 6*a*, *c*, *e*, $\times 100$. Figs 6*b*, *d*, and 7*a*, *b*, $\times 185$

- Fig. 6. *Aptenodytes pennanti*.
a. Distal barbule from near base of barb of back feather.
b. Same. $\times 185$.
c. Proximal barbule from near base of barb of back feather.
d. Same. $\times 185$.
e. Portion of barb from aftershaft.
- Fig. 7. *Eudyptes chrysocome*.
a. Distal barbule from near base of barb of back feather.
b. Proximal barbule from same.

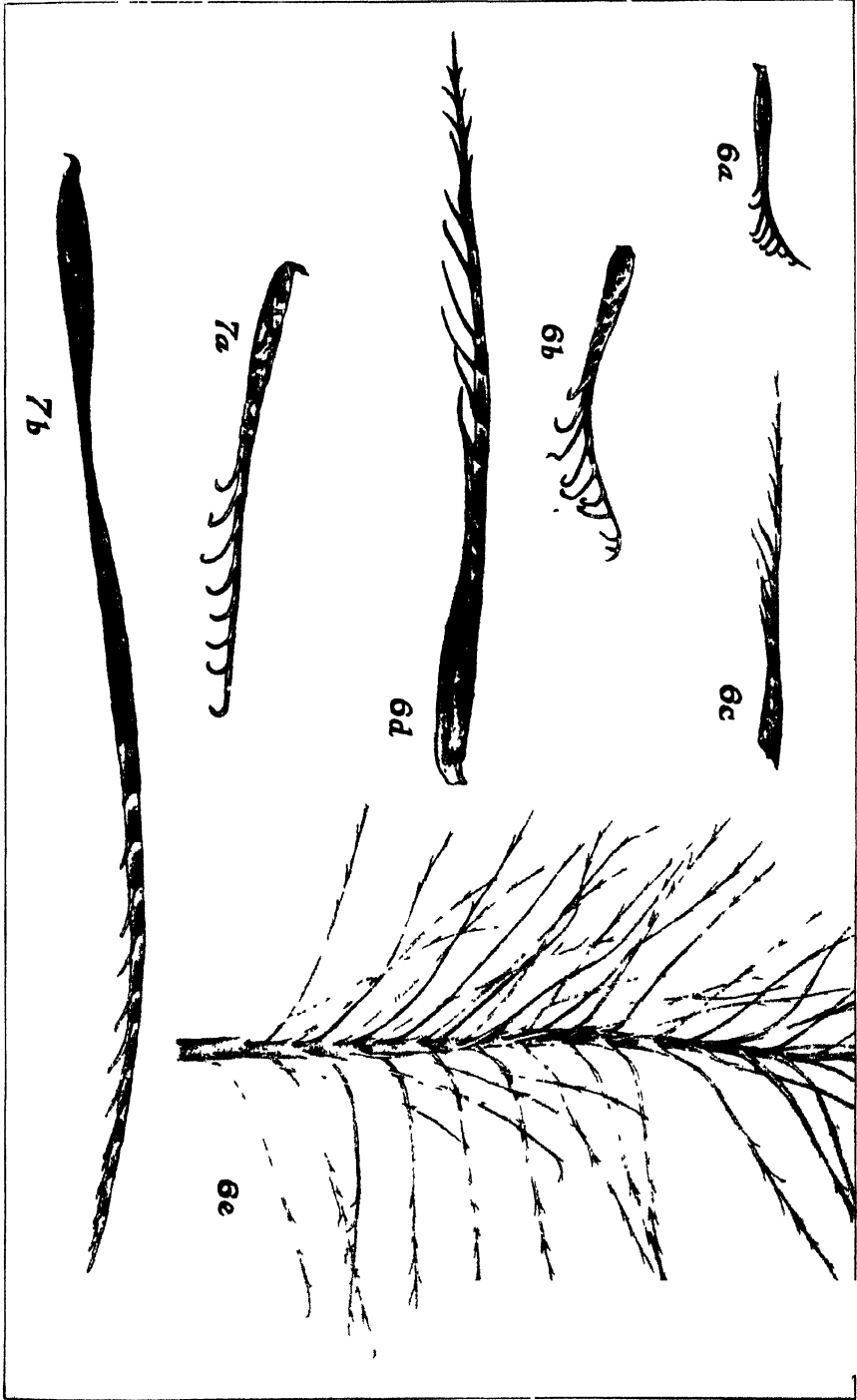


PLATE 16

COLYMBIFORMES

All figures, except 9h, \times 100

- Fig. 8. *Gavia immer*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex, pennulum in lateral view.
d. Proximal barbule from same distal third of barb.
e. Distal barbule from breast feather.
f. Proximal barbule from same.
- Fig. 9. *Aechmophorus occidentalis*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex.
d. Proximal barbule from same, distal third of barb.
e. Distal barbule from back feather.
f. Proximal barbule from same.
g. Distal barbule from back feather, near tip of barb.
h. Portion of barb from breast feather. \times 36.

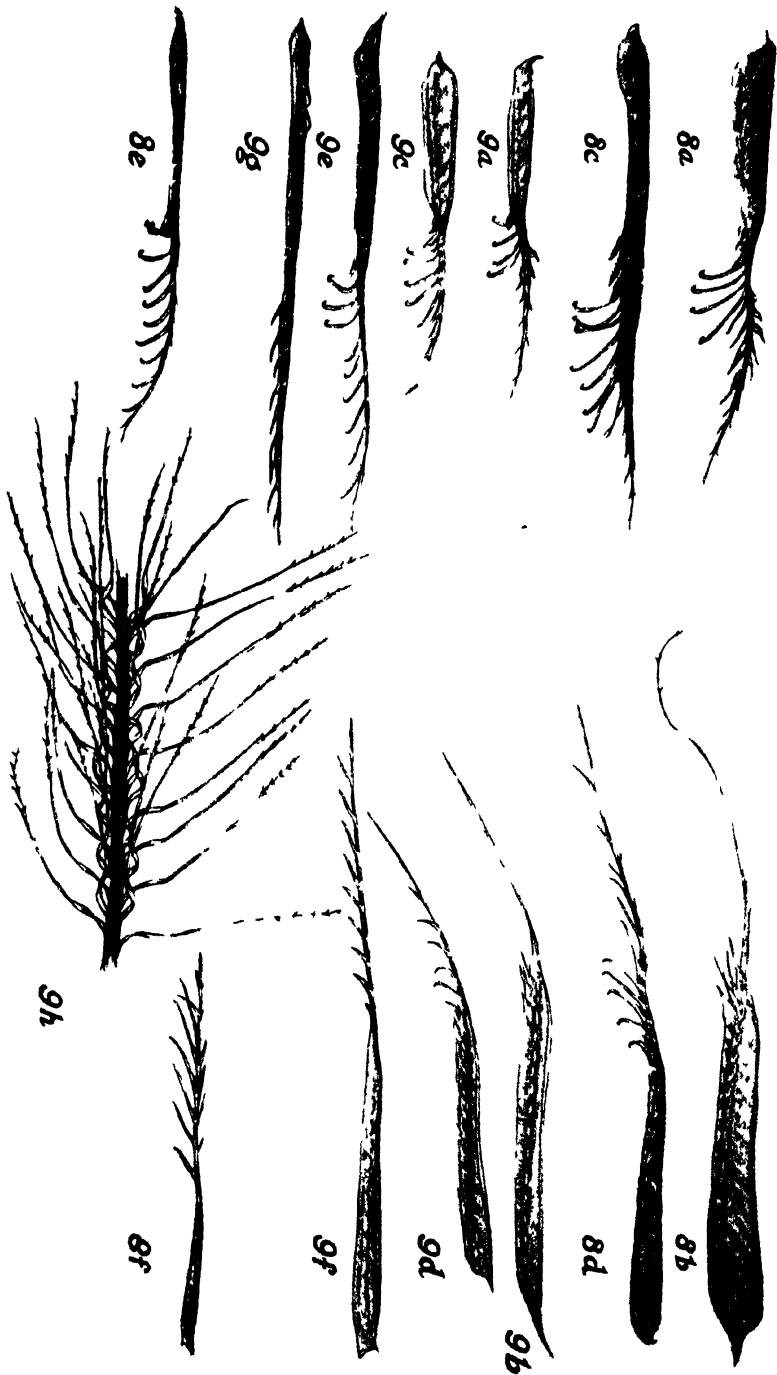


PLATE 17

PROCELLARIIFORMES

All figures $\times 100$

- Fig. 10. *Diomedea exsulans*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex.
d. Proximal barbule from same, distal third of barb.
e. Distal barbule from outer third of barb of breast feather.
- Fig. 11. *Puffinus griseus*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Proximal barbule from outer vane of remex, distal third of barb.
- Fig. 12. *Oceanodroma melania*.
a. Distal barbule from near tip of barb of breast feather.
b. Proximal barbule from same.

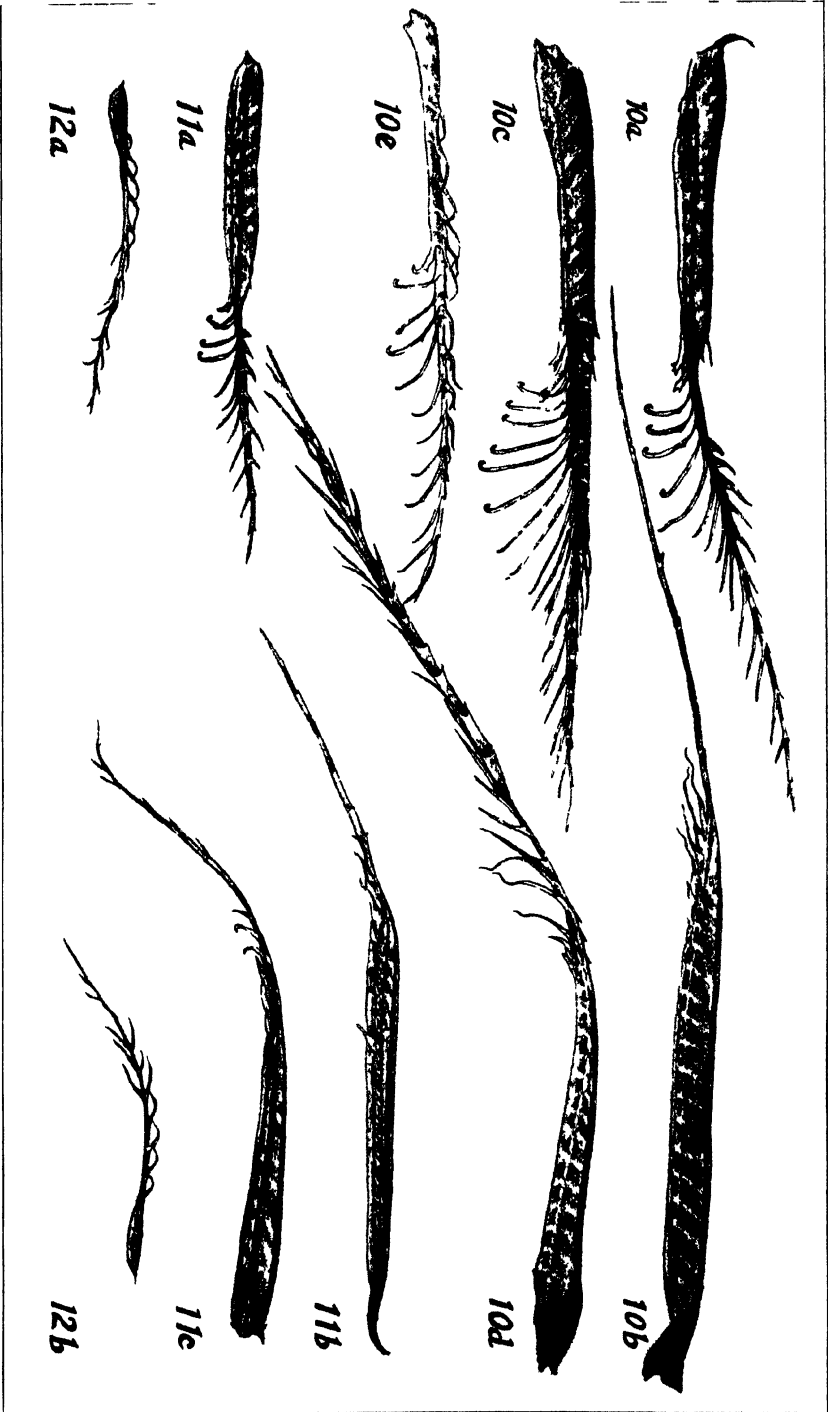


PLATE 18

STEGANOPODES

All figures $\times 100$

- Fig. 13. *Plotus anhinga*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex, silvery gray portion.
d. Proximal barbule from same, distal third of barb.
e. Distal barbule from back feather, silvery gray portion.
f. Distal barbule from back feather, black portion.
g. Proximal barbule from back feather, about middle of barb.
- Fig. 14. *Phalacrocorax penicillatus*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex.
d. Proximal barbule from same, distal third of barb.
e. Distal barbule from back feather, velvety portion.
f. Proximal barbule from same.
- Fig. 15. *Fregata aquila*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.

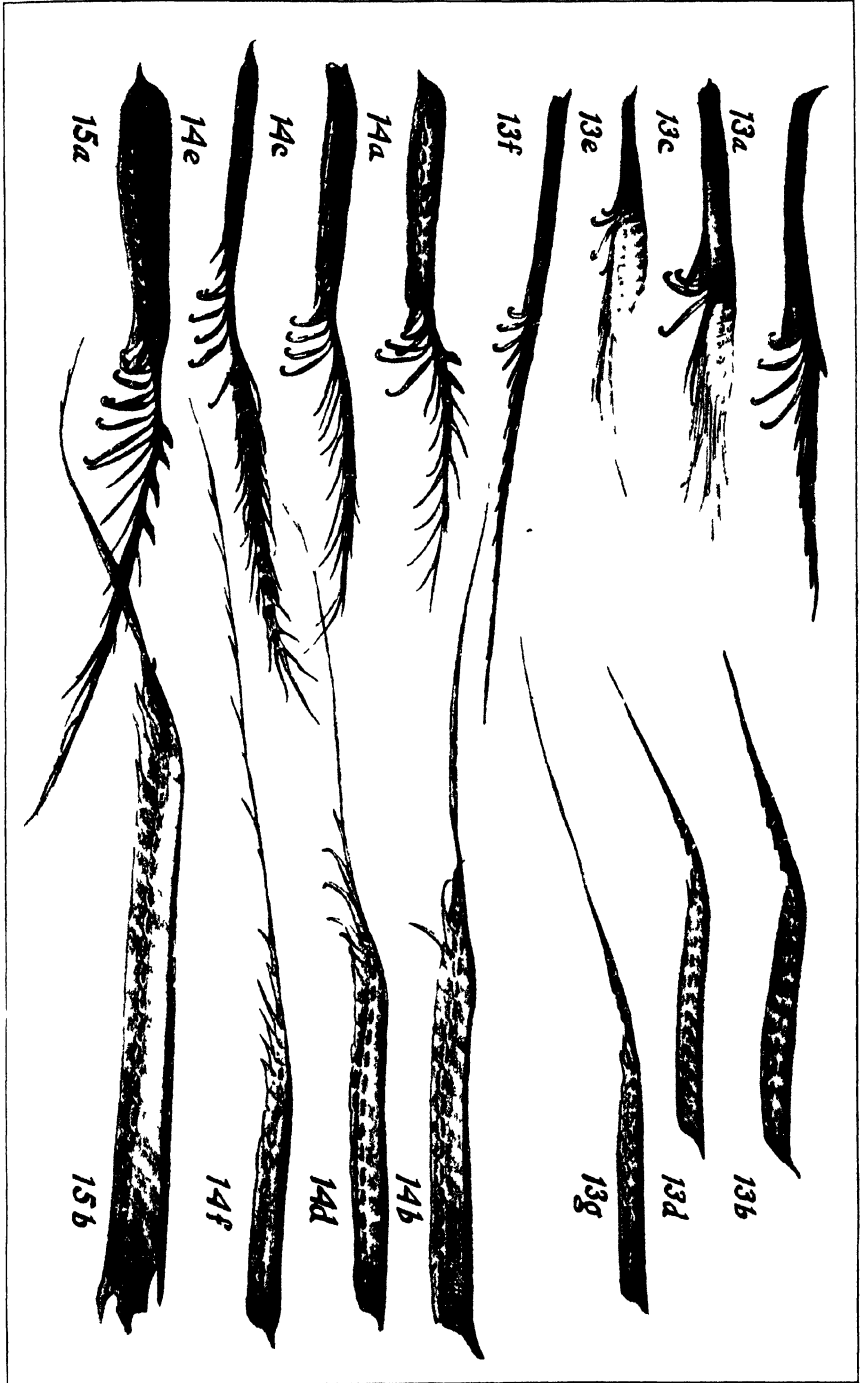


PLATE 19

STEGANOPODES, *continued*

All figures $\times 100$

- Fig. 16. *Sula variegata*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from back feather.
d. Proximal barbule from same.
- Fig. 17. *Pelecanus erythrorhynchus*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Proximal barbule from outer vane of remex.
d. Distal barbule from breast feather, distal third of barb.
e. Proximal barbule from breast feather, proximal third of barb.
- Fig. 18. *Pelecanus californicus*.
a. Distal barbule from back feather, velvety portion.
- Fig. 19. *Phaethon flaviventris*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex.
d. Proximal barbule from same, distal third of barb.
e. Distal barbule from breast feather, near tip of barb.
f. Proximal barbule from same.

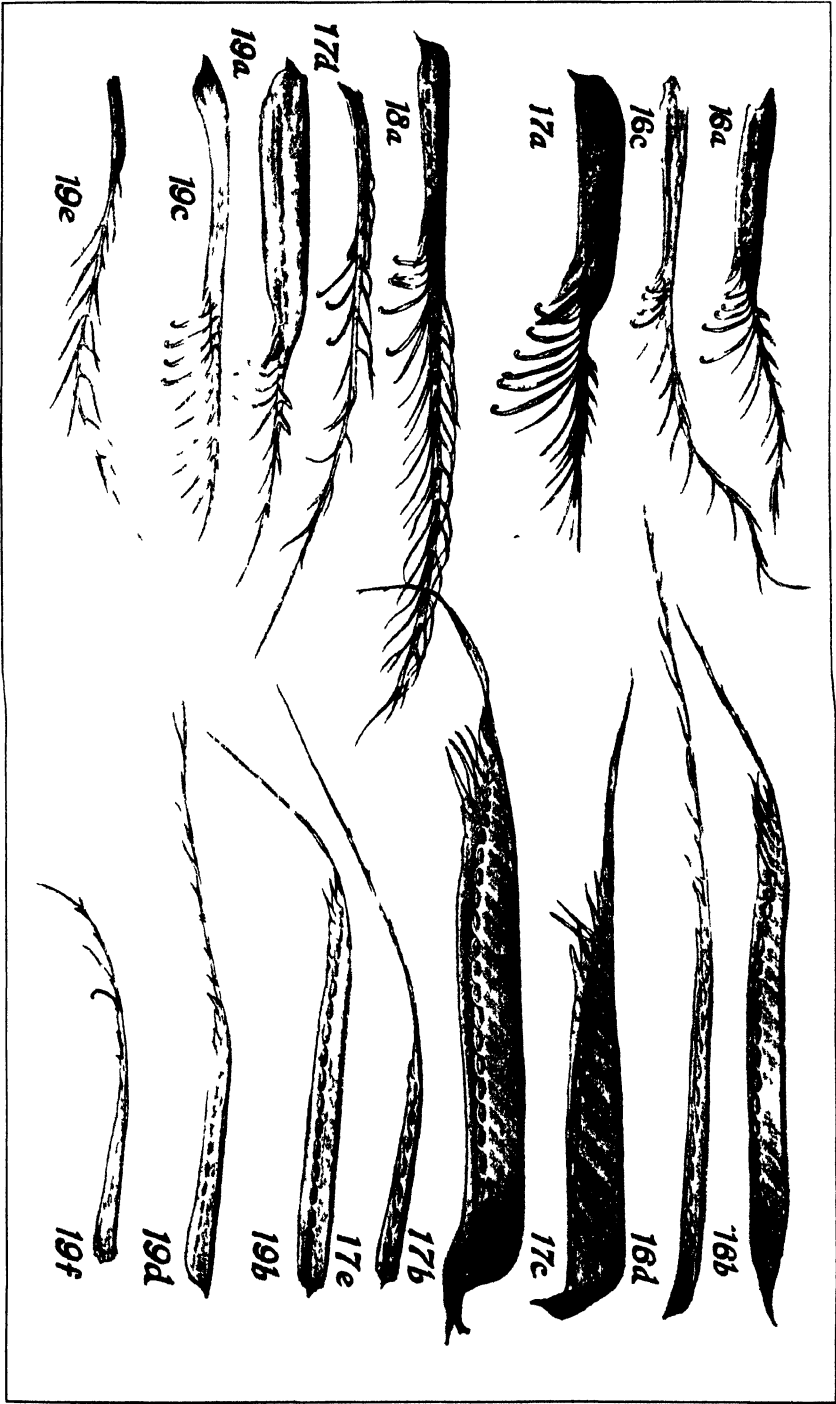


PLATE 20

ARDEAE AND CICONIAE

All figures $\times 100$

- Fig. 20. *Ardea herodias*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex.
d. Proximal barbule from same, distal third of barb.
e. Distal barbule from back feather, basal third.
f. Proximal barbule from same.
- Fig. 21. *Butorides virescens*.
a. Distal barbule from outer vane of remex.
b. Proximal barbule from same, distal third of barb.
- Fig. 22. *Egretta candidissima*.
a. Barbule from "aigrette."
- Fig. 23. *Mycteria americana*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex.
d. Distal barbule from breast feather.
- Fig. 24. *Leptoptilus dubius*.
a. Distal barbule from inner vane of remex.
b. Distal barbule from outer vane of remex.
- Fig. 25. *Plegadis guarauna*.
a. Distal barbule from inner vane of remex.
- Fig. 26. *Guara (Eudocimus) ruber*.
a. Distal barbule from scarlet back feather.
- Fig. 27. *Ajaja ajaja*.
a. Distal barbule from back feather.

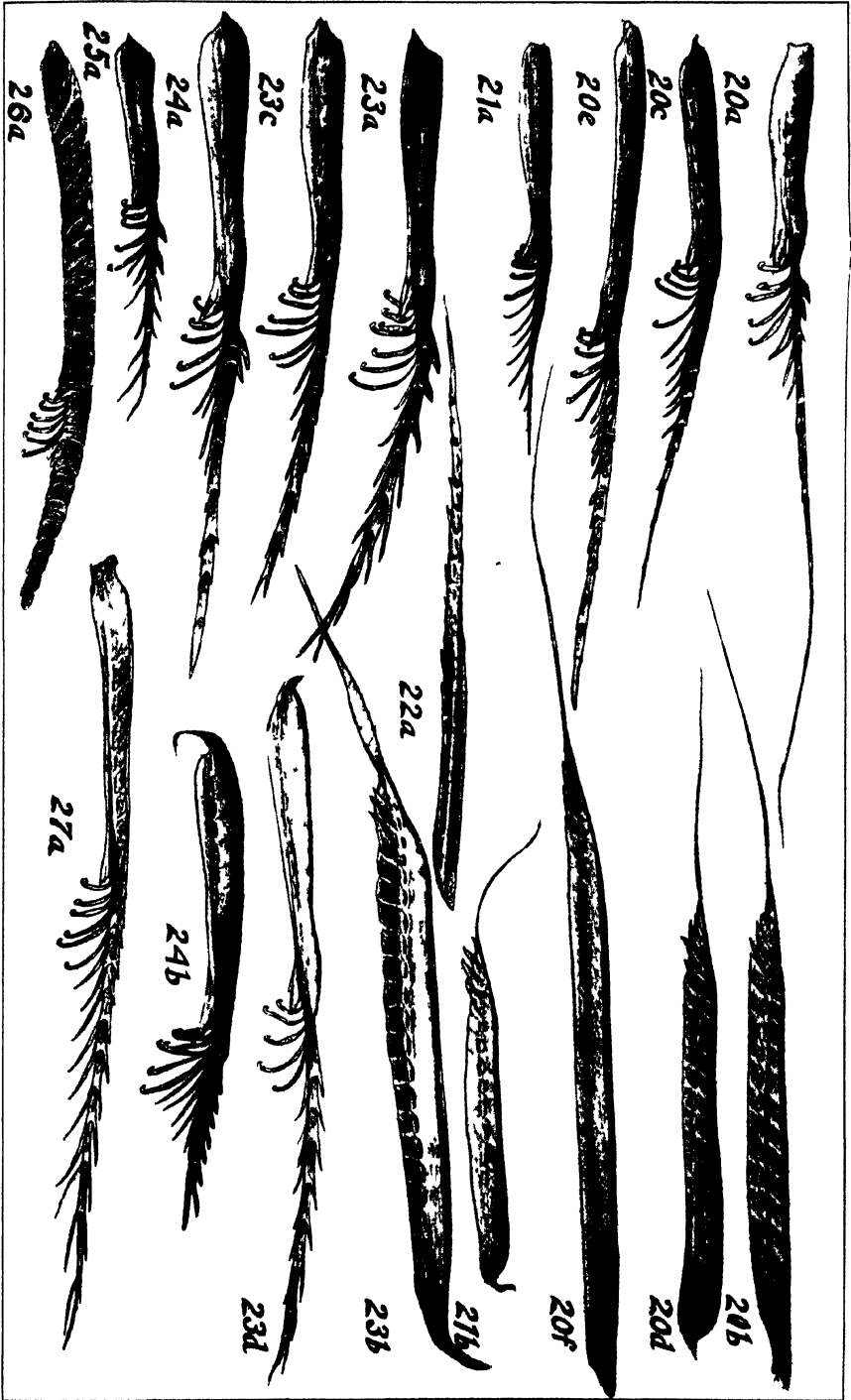


PLATE 21

ANSERIFORMES AND PHOENICOPTERI

All figures, except 28*a* and *b*, $\times 100$

- Fig. 28. *Anas platyrhynchos*.
a. Basal portion of barb from inner vane of primary. $\times 8$.
b. Portion of ventral part of basal region of barb, from outer vane of primary. $\times 120$.
c. Distal barbule from inner vane of remex.
d. Proximal barbule from same.
e. Distal barbule from outer vane of remex.
f. Proximal barbule from same, distal third of barb.
g. Distal barbule from outer vane of tail feather.
h. Proximal barbule from same, distal third of barb.
i. Distal barbule from outer vane of violet speculum feather.
- Fig. 29. *Nettion carolinense*.
a. Distal barbule from outer vane of primary.
b. Distal barbule from outer vane of green speculum feather.
c. Proximal barbule from same, distal third of barb.
- Fig. 30. *Mareca americana*.
a. Distal barbule from outer velvety black vane of scapular feather.
- Fig. 31. *Chauna cristata*.
a. Distal barbule from outer vane of remex.
b. Proximal barbule from same.
- Fig. 32. *Phoenicopterus ruber*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from outer vane of remex, distal third of barb.
c. Proximal barbule from scapular feather, distal half of barb.



PLATE 22

FALCONIFORMES

All figures $\times 100$

- Fig. 33.** *Gyps fulvus*.
a. Distal barbule from back feather.
b. Proximal barbule from same.
c. Distal barbule from outer vane of primary.
d. Proximal barbule from same, distal third of barb.
- Fig. 34.** *Gymnogyps californianus*.
a. Distal barbule from inner vane of remex.
b. Same, with pennulum in lateral view.
c. Proximal barbule from inner vane of remex.
d. Distal barbule from outer vane of remex.
e. Proximal barbule from same, distal third of barb.
- Fig. 35.** *Gypogeranus serpentarius*.
a. Distal barbule from blue-gray scapular feather.
b. Proximal barbule from same.
c. Distal barbule from inner vane of remex.
d. Proximal barbule from same.



PLATE 23

FALCONIFORMES (Accipitres)

All figures $\times 100$

- Fig. 36. *Falco peregrinus*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Proximal barbule from outer vane of remex.
- Fig. 37. *Falco sparverius*.
a. Distal barbule from inner vane of remex.
- Fig. 38. *Buteo borealis*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Proximal barbule from outer vane of remex.
- Fig. 39. *Haliaeetus leucocephalus*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
- Fig. 40. *Polyborus cheriway*.
a. Distal barbule from inner vane of remex.
- Fig. 41. *Falco rusticola*.
a. Distal barbule from back feather.
b. Proximal barbule from same.

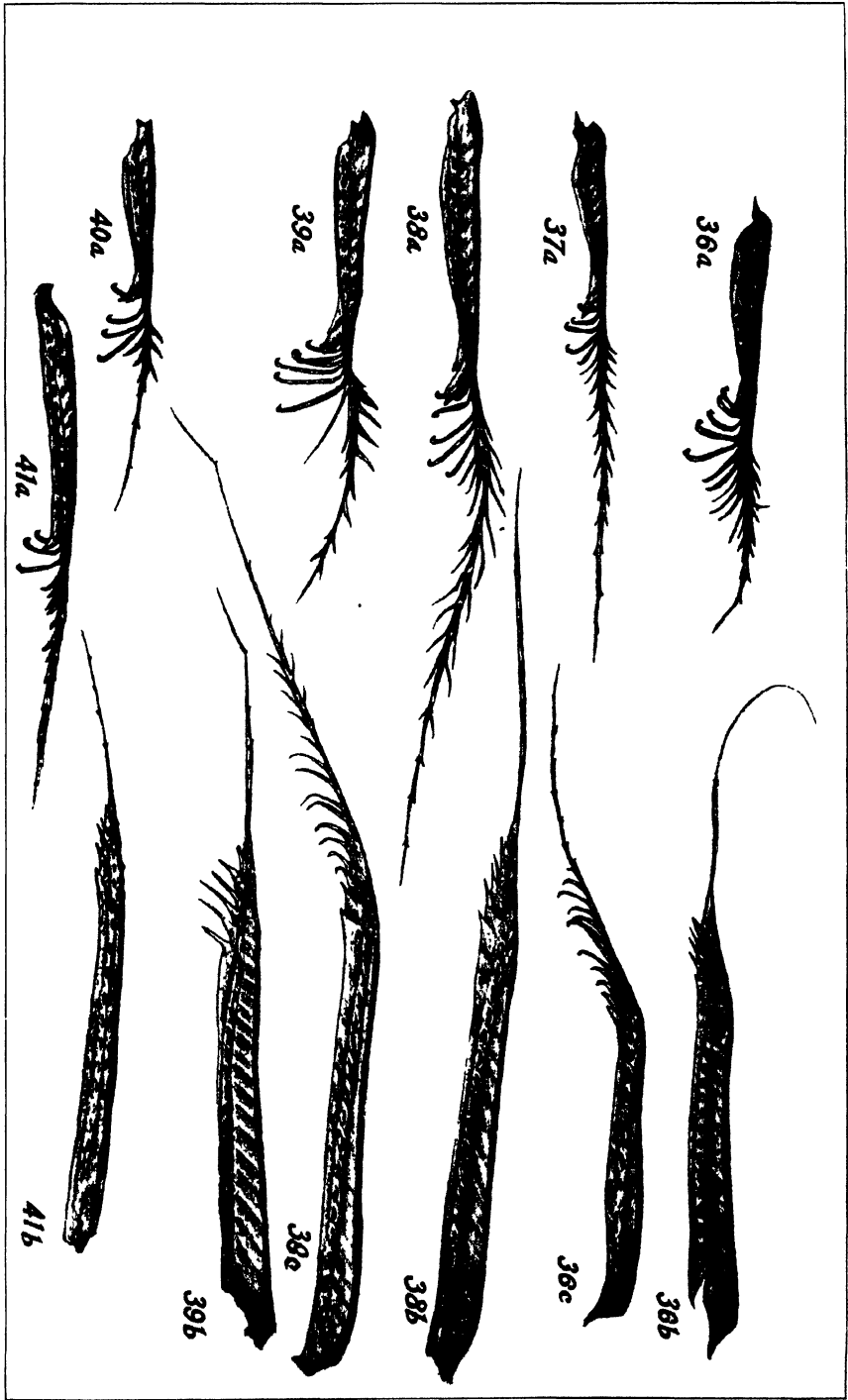


PLATE 24

GALLIFORMES

All figures $\times 100$

- Fig. 42. *Gallus domesticus*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex.
d. Proximal barbule from same, about middle of length of barb.
e. Proximal barbule from same, distal fourth of barb.
f. Proximal barbule from back feather.
g. Distal barbule from iridescent green tail plume.
- Fig. 43. *Bonasa umbellus*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Proximal barbule from outer vane of remex.
- Fig. 44. *Meleagris virginiana*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
- Fig. 45. *Megapodius cumingi*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from outer vane of remex, distal third of barb.
- Fig. 46. *Penelope cristata*.
a. Distal barbule from inner vane of remex.
- Fig. 47. *Lagopus lagopus*.
a. Distal barbule from white back feather.
- Fig. 48. *Turnix lepurana*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.

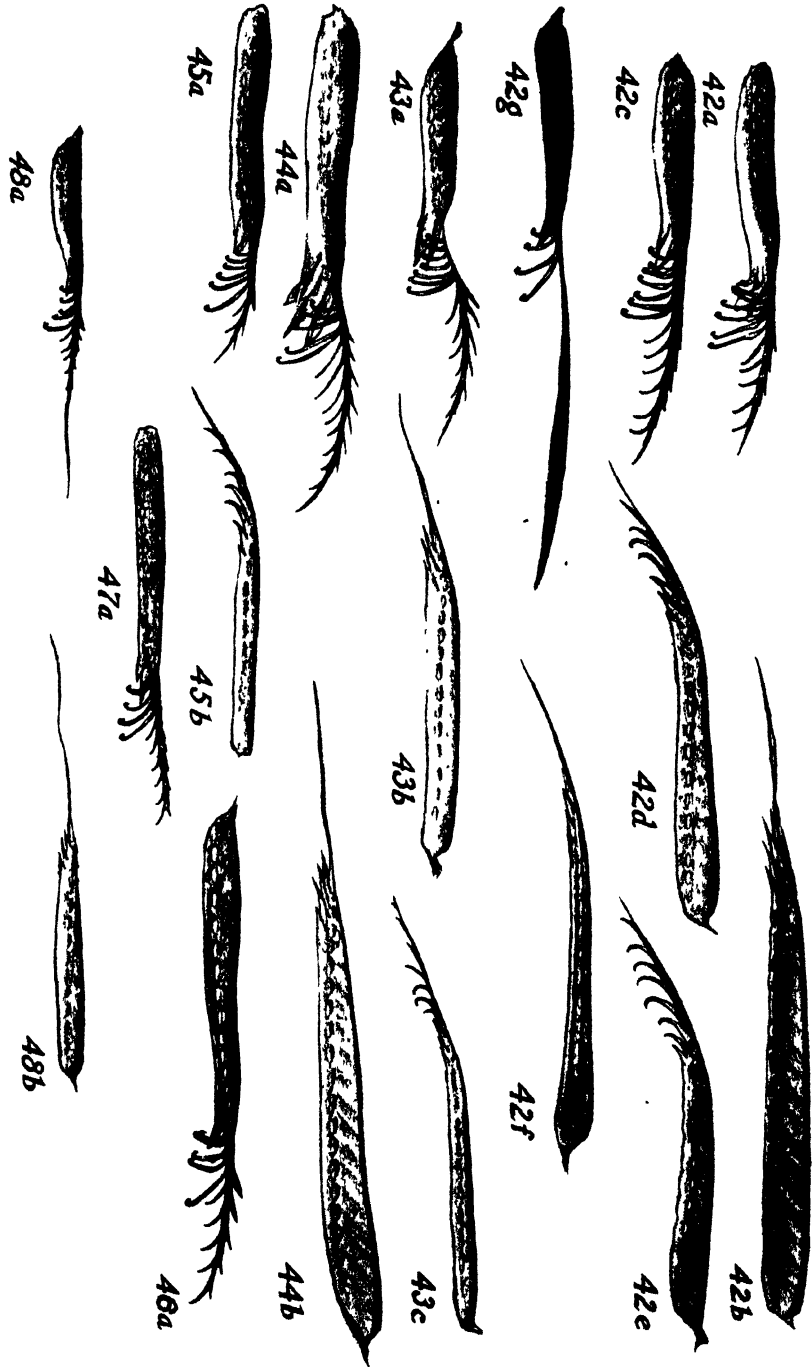


PLATE 25

CRYPTURIFORMES

All figures $\times 135$

Fig. 49. *Tinamus solitarius*.

- a. Distal barbule from inner vane of remex.
- b. Portion of proximal barbule, from inner vane of remex.
- c. Distal barbule from outer vane of remex.
- d. Distal barbule from back feather, black.
- e. Portion of proximal vanule, from breast feather.
- f. Basal portion of down barbule, from back feather.

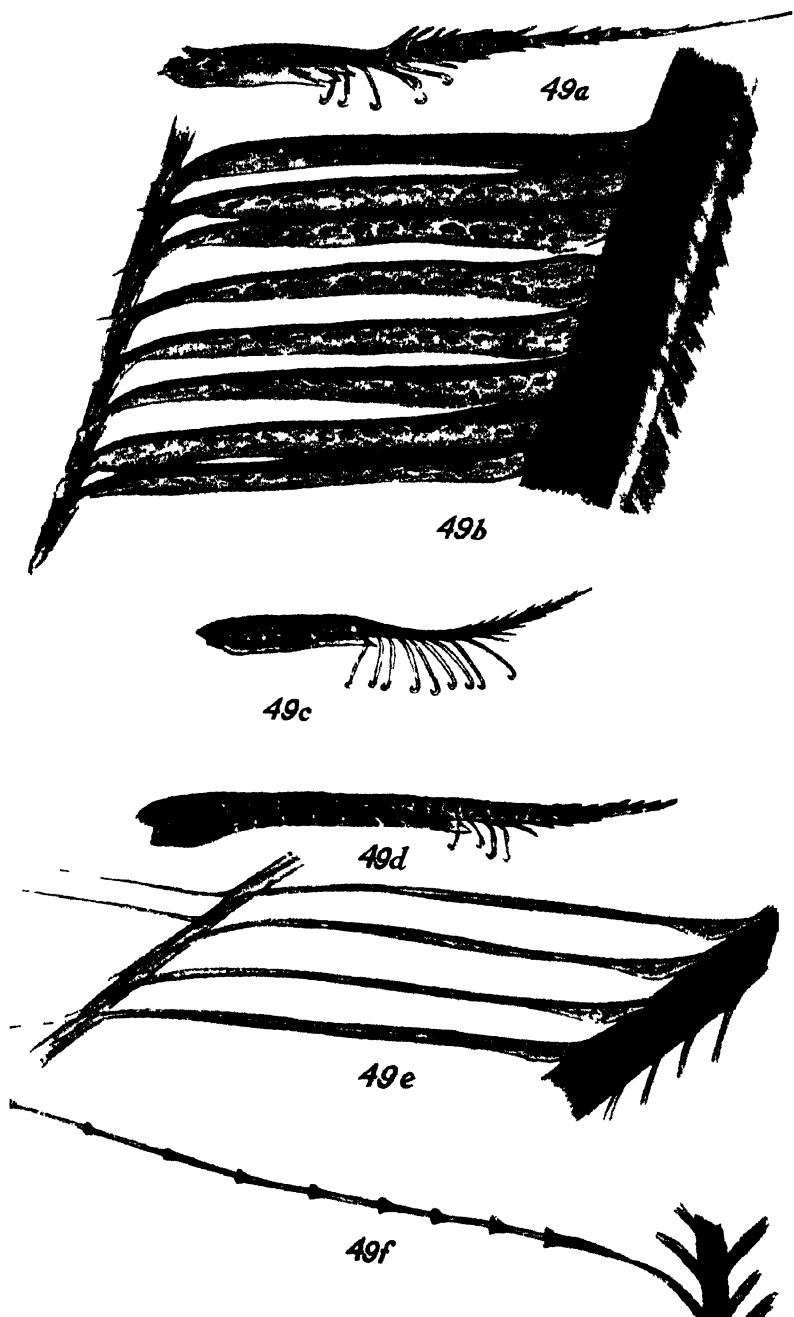


PLATE 26

GRUIFORMES

All figures $\times 100$

Fig. 50. *Grus canadensis*.

- a. Distal barbule from inner vane of remex.
- b. Distal barbule from outer vane of remex.
- c. Proximal barbule from same.
- d. Proximal barbule from back feathers.
- e. Distal barbule from breast feather, proximal half of barb.
- f. Barbule, distal or proximal, from breast feather, distal third of barb.

Fig. 51. *Aramus giganteus*.

- a. Distal barbule from back feather, proximal half of barb.
- b. Proximal barbule from same.
- c. Distal barbule from breast feather, about middle of barb.
- d. Proximal barbule from same, about middle of barb.
- e. Barbule, distal or proximal, from breast feather, distal third of barb.

Fig. 52. *Rallus obsoletus*.

- a. Distal barbule from inner vane of remex.
- b. Proximal barbule from same.
- c. Proximal barbule from outer vane of remex.
- d. Distal barbule from breast feather, about end of proximal third of barb.
- e. Distal barbule from same, about middle of barb.
- f. Distal barbule from same, distal third of barb.
- g. Proximal barbule from same, about end of proximal third of barb.
- h. Proximal barbule from same, distal third of barb.

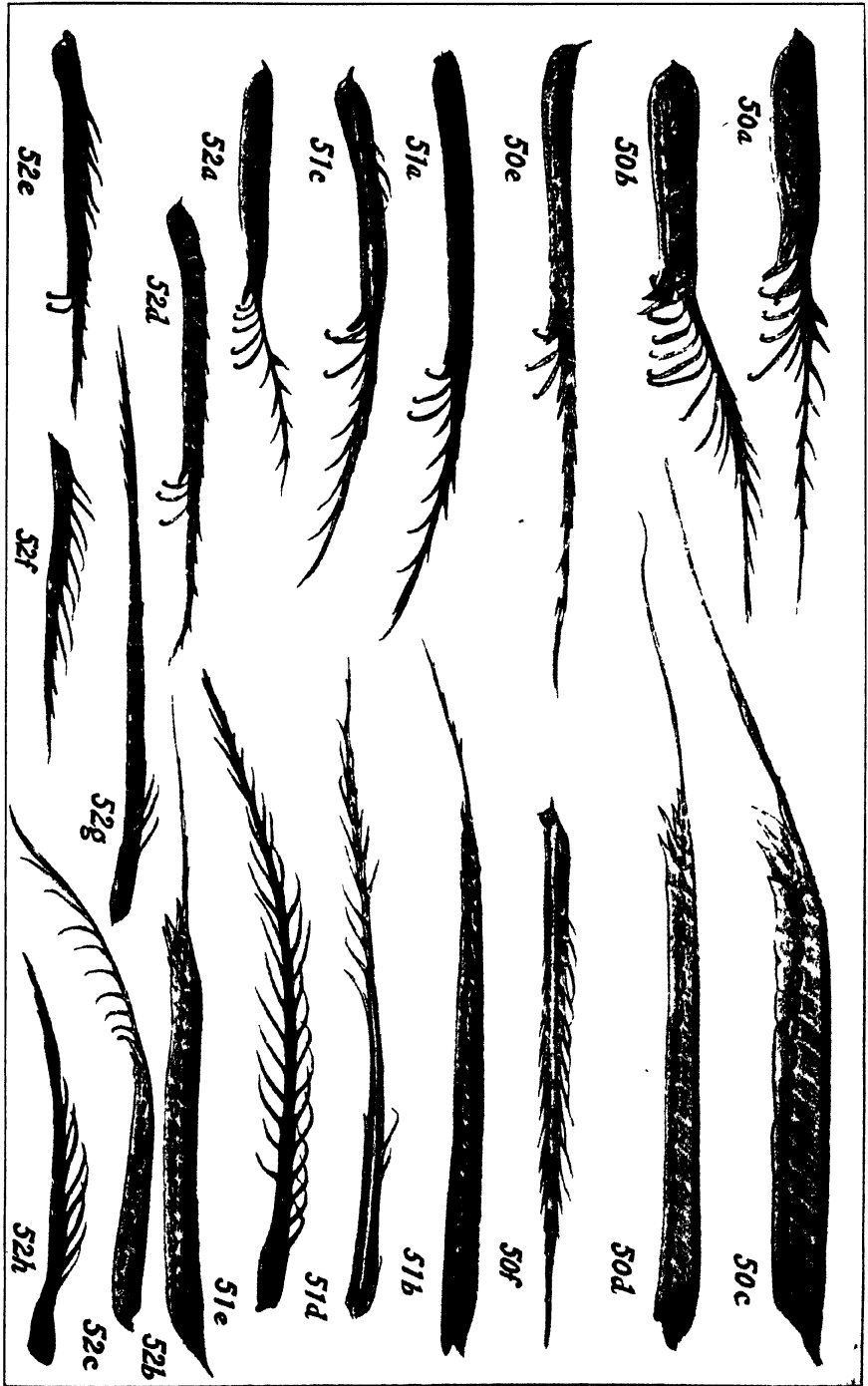


PLATE 27

GRUIFORMES, *continued*

All figures $\times 100$

- Fig. 53.** *Otis tarda*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from back feather.
d. Proximal barbule from back feather.
- Fig. 54.** *Psophia viridis*.
a. Distal barbule from inner vane of greater covert.
b. Proximal barbule from outer vane of greater covert.
c. Distal barbule from back feather.
d. Proximal barbule from back feather.
e. Barbule from iridescent green portion of outer vane of covert.
- Fig. 55.** *Eurypyga helias*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from back feather.
d. Proximal barbule from back feather.
- Fig. 56.** *Cariama cristata*.
a. Distal barbule from back feather, near base of barb.
b. Proximal barbule from same.

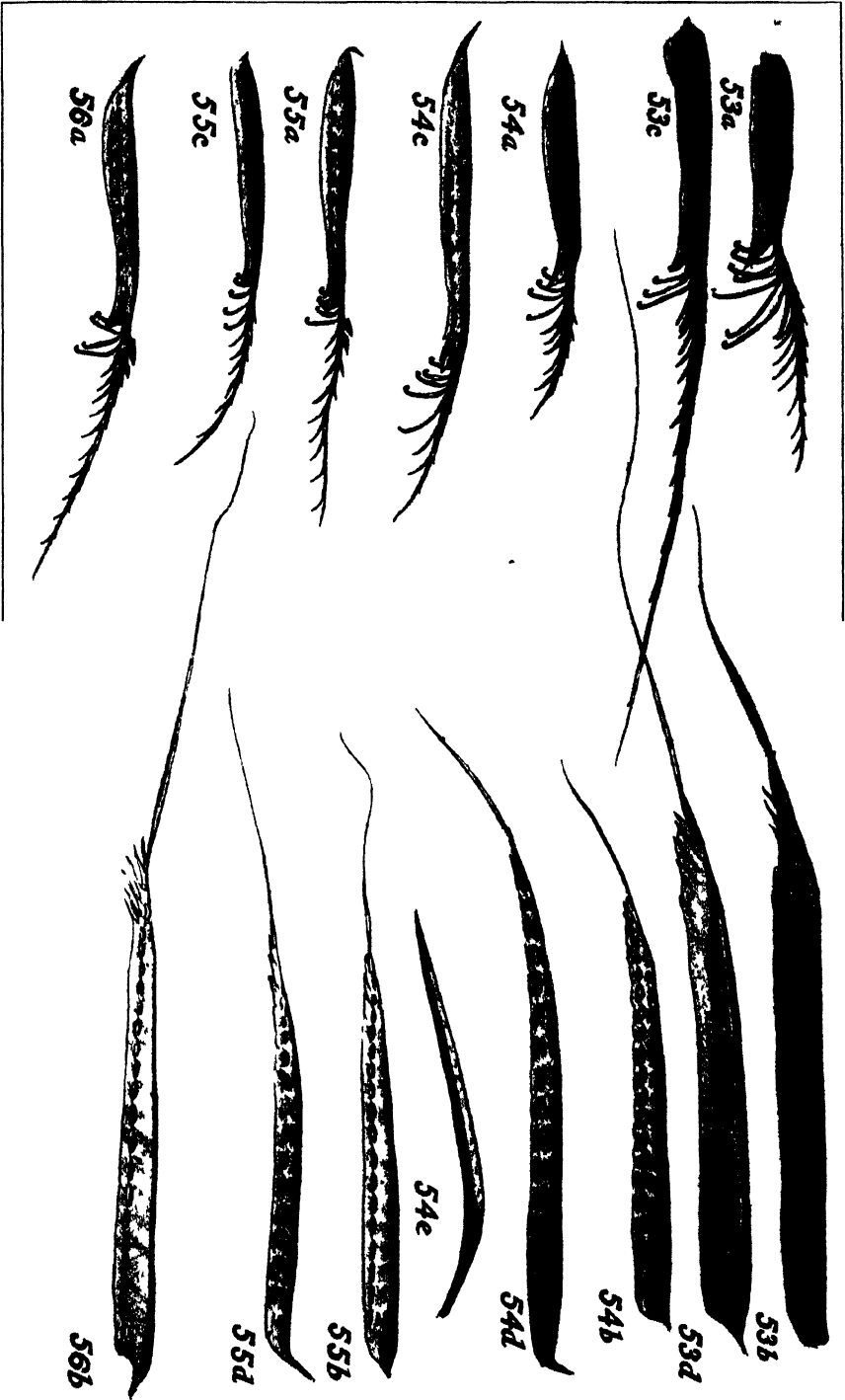


PLATE 28

LABO-LIMICOLAE

All figures $\times 100$

- Fig. 57. *Numenius americanus*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex.
d. Proximal barbule from same, distal fourth of barb.
e. Distal barbule from back feather.
f. Barbule, distal or proximal, from breast feather, distal half of barb.
- Fig. 58. *Parra spinosa*.
a. Distal barbule from back feather, near base of barb.
b. Same, distal third of barb.
- Fig. 59. *Phalaropus fulicarius*.
a. Barbule from breast feather, distal third of barb.
- Fig. 60. *Cursorius gallicus*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from breast feather, near tip of barb.
- Fig. 61. *Larus occidentalis*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex.
d. Proximal barbule from same, distal fourth of barb.
e. Barbule from breast feather, distal third of barb.
- Fig. 62. *Sterna maxima*.
a. Distal barb from outer vane of remex.
- Fig. 63. *Uria troille*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex.
d. Distal barbule from breast feather, near base of barb.
e. Same, near tip of barb.
f. Proximal barbule of same, near tip of barb.

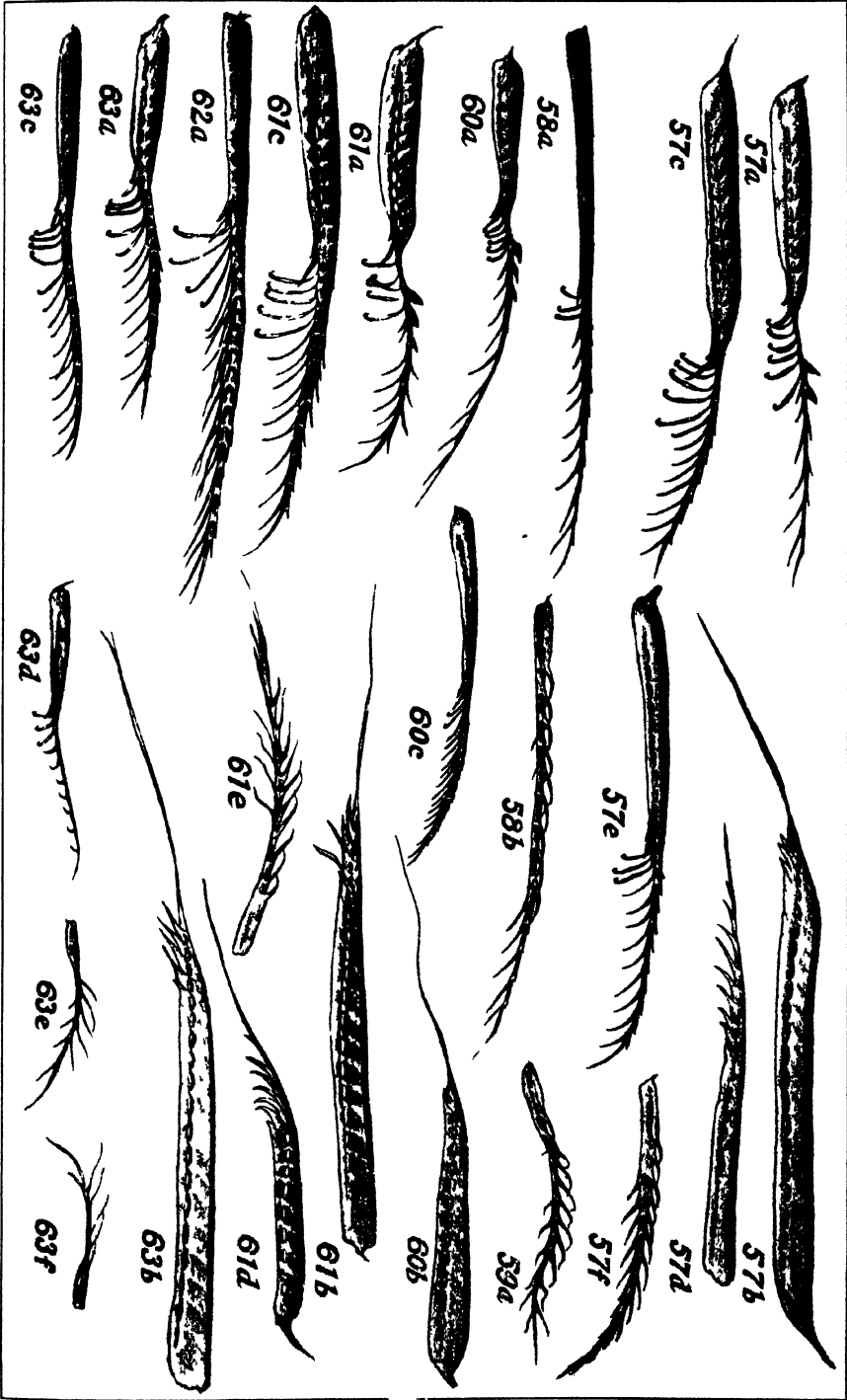


PLATE 29

PTEROCLO-COLUMBAE

All figures, except 67a, $\times 100$

- Fig. 64. *Columba livia*.
a. Distal barbule from inner vane of remex, white.
b. Proximal barbule from same, white.
c. Distal barbule from outer vane of remex, slate gray.
- Fig. 65. *Zenaidura macroura*.
a. Distal barbule from olive brown back feather.
- Fig. 66. *Melopelia asiatica*.
a. Distal barbule from blue-gray covert.
b. Distal barbule from breast feather, pearl gray.
c. Proximal barbule from same.
- Fig. 67. *Columba fasciata*.
a. Hooklet region of distal barbule from covert. $\times 480$.
b. Barbule from iridescent green neck feather.
- Fig. 68. *Macropygia tenuirostris*.
a. Distal barbule from rufous under tail covert.
- Fig. 69. *Osmotreron vernans*.
a. Distal barbule from olive green covert.
- Fig. 70. *Goura coronata*.
a. Distal barbule from inner vane of remex, slate blue.
b. Proximal barbule from same.
c. Distal barbule from back feather, grayish blue.
d. Proximal barbule from same.
e. Barbule from loose barb of decomposed crest feather.
- Fig. 71. *Pteroclis arenarius*.
a. Distal barbule from inner vane of remex.
b. Distal barbule from outer vane of scapular feather.
c. Proximal barbule from same.

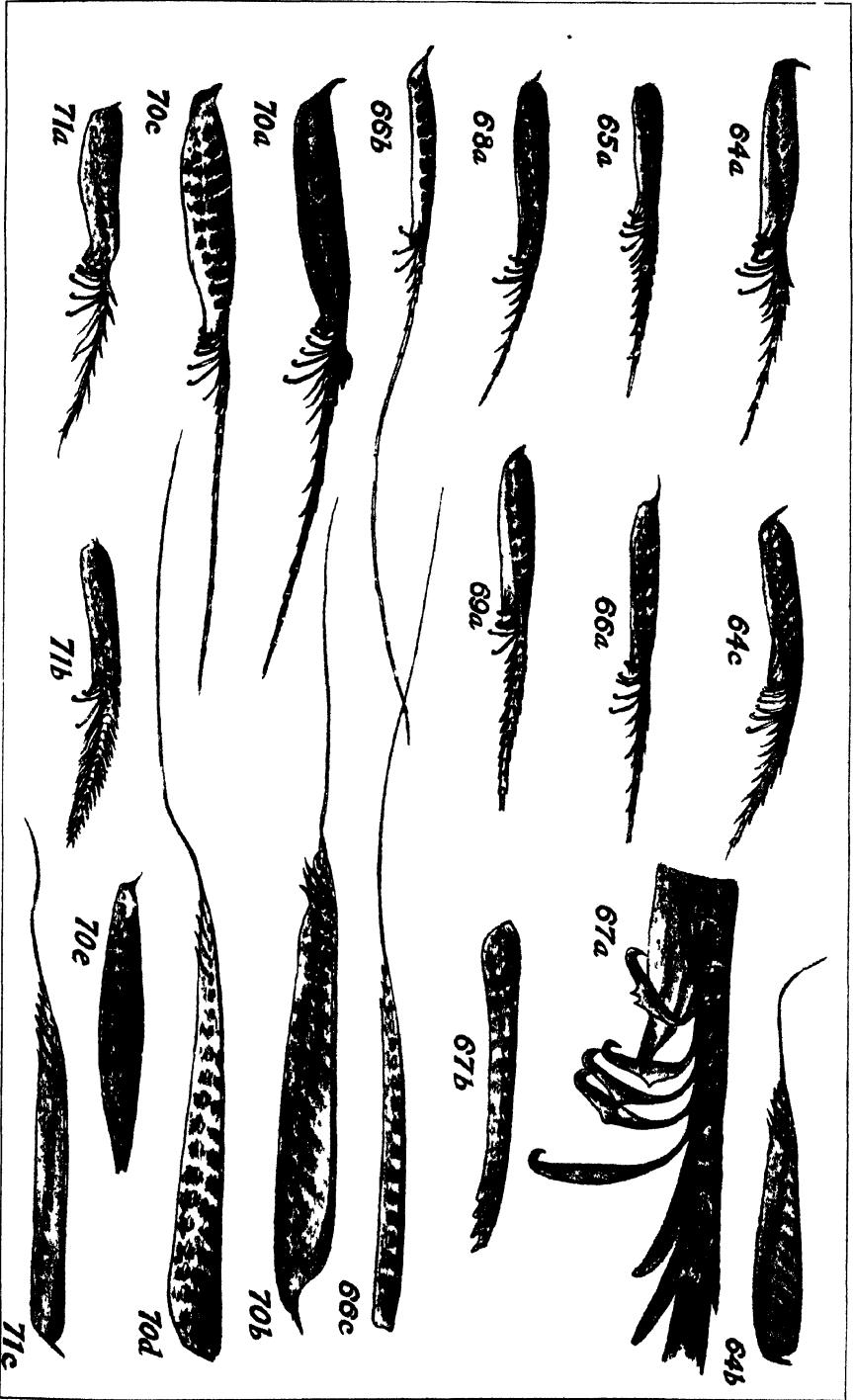


PLATE 30

CUCULIFORMES

All figures $\times 125$

- Fig. 72. *Coccyzus americanus*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex.
d. Proximal barbule from same.
e. Distal barbule from breast feather.
f. Proximal barbule from same.
- Fig. 73. *Geococcyx californianus*.
a. Proximal barbule from glossy green outer vane of remex.
- Fig. 74. *Cacatua galerita*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from same.
d. Proximal barbule from same, distal third of barb.
- Fig. 75. *Melopsittacus* sp.
a. Distal barbule from outer vane of remex.
b. Proximal barbule from same, distal third of barb.
- Fig. 76. *Tanygnathus lucionensis*.
a. Distal barbule from yellowish-olive-green back feather.
- Fig. 77. *Aprostinictus cyanopygius*.
a. Distal barbule from red belly feather.
b. Proximal barbule from same.

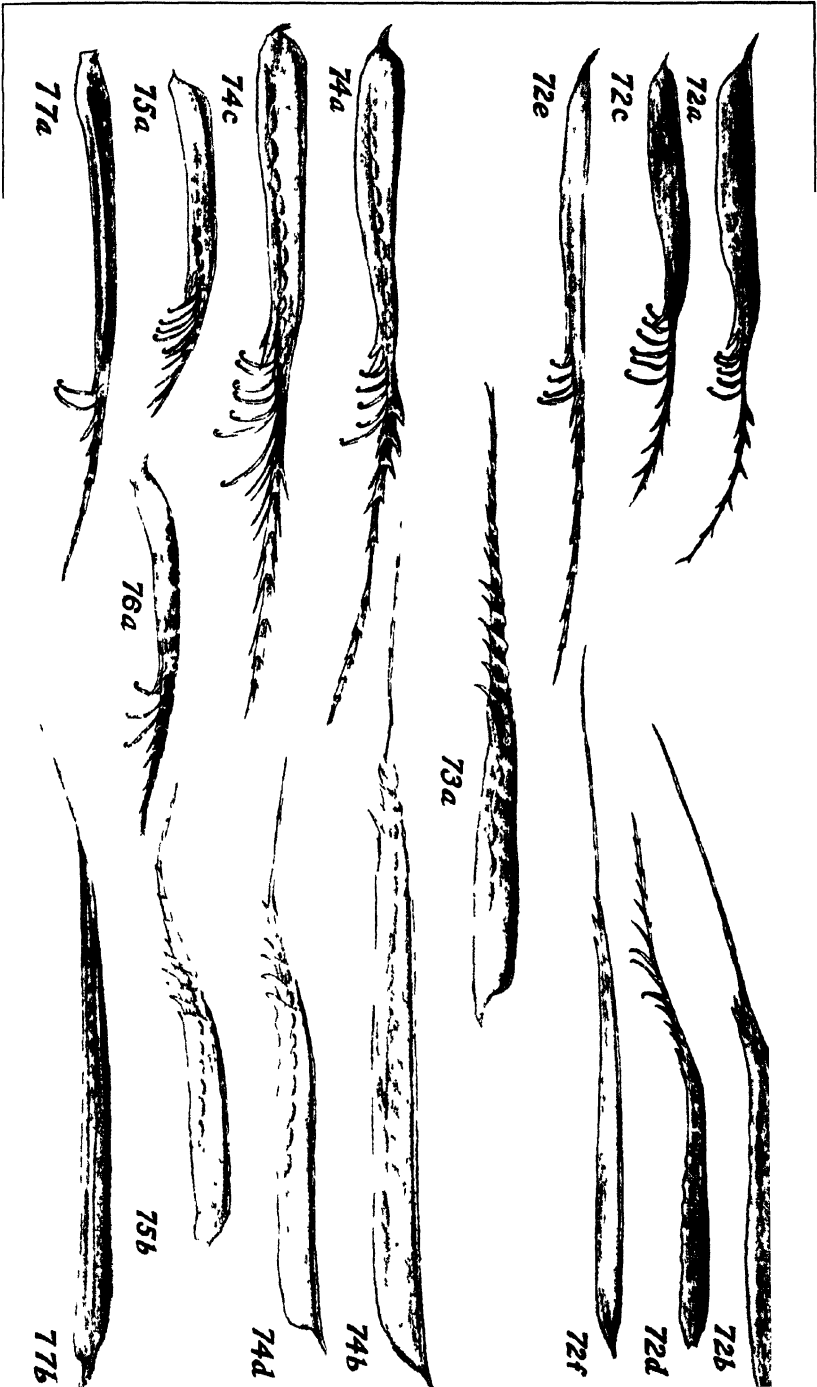


PLATE 31

CORACIIFORMES (Coraciæ and Trogones)

All figures $\times 100$

- Fig. 78. *Coracias affinis*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Proximal barbule from outer vane of remex.
- Fig. 79. *Ceryle alcyon*.
a. Proximal barbule from outer vane of remex, distal half of barb.
b. Proximal barbule from breast feather.
- Fig. 80. *Prionotelus temnurus*.
a. Distal barbule from inner vane of remex.
b. Distal barbule from outer vane of remex.
c. Proximal barbule from same, distal third of barb.
- Fig. 81. *Phaeromacrus resplendens*.
a. Barbule from brilliant green ornamental upper tail covert.
- Fig. 82. *Hydrocorax mindanensis*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex.
d. Same, with pennulum in lateral view.
e. Proximal barbule from outer vane of remex, distal third of barb.
- Fig. 83. *Irrisor viridis*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from outer vane of remex, distal third of barb.

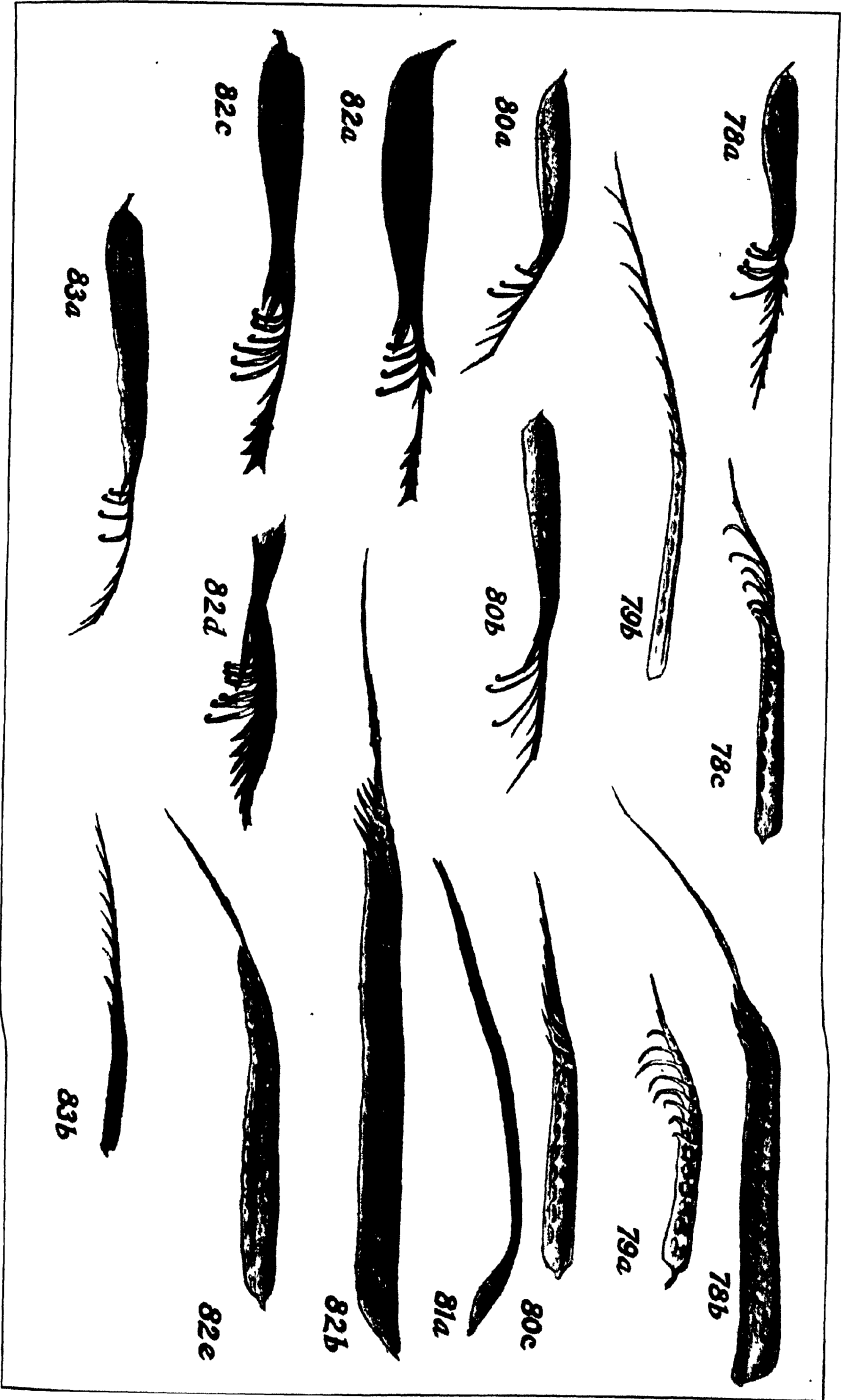


PLATE 32

CORACIIFORMES. (Striges, Caprimulgi, Cypseli)

All figures, except 88b, c, and d, $\times 100$

- Fig. 84. *Bubo virginianus*.
a. Distal barbule from inner vane of primary.
b. Proximal barbule from same.
c. Proximal barbule from outer vane, on distal, recurved, tooth-like portion of barb.
- Fig. 85. *Aluco pratincola*.
a. Distal barbule from breast feather.
- Fig. 86. *Chordeiles virginianus*.
a. Distal barbule from outer vane of remex.
b. Proximal barbule from same, distal third of barb.
- Fig. 87. *Podargus strigoides*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
- Fig. 88. *Selasphorus rufus*.
a. Distal barbule from outer vane of primary.
b. Same, $\times 275$.
c. Proximal barbule from outer vane of primary. $\times 275$.
d. Proximal barbule from iridescent fiery-red gorget feather. $\times 275$.

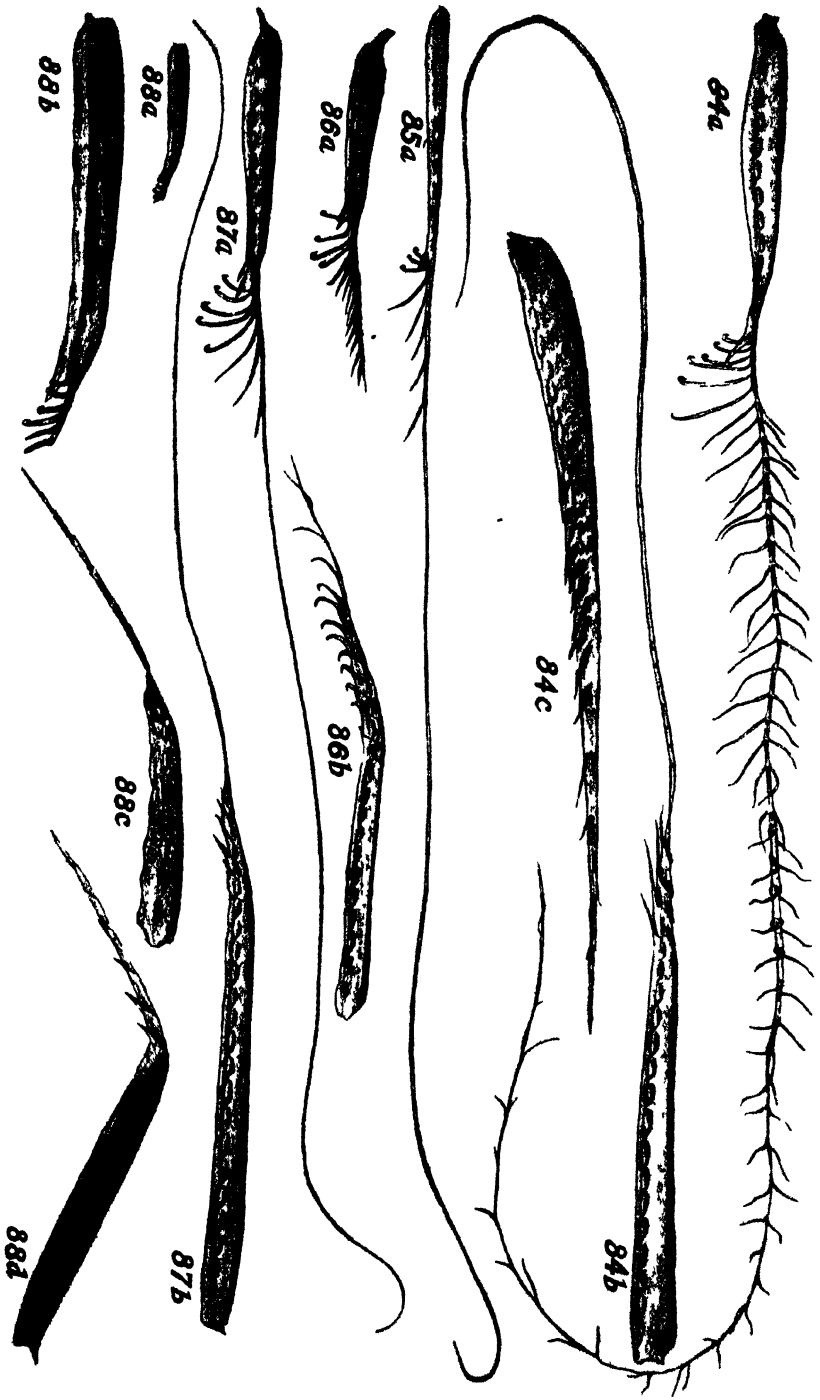


PLATE 33

PICID AND PASSERIFORMES

All figures, except 95a, \times 125

- Fig. 89. *Melanerpes formicivorus*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex.
d. Proximal barbule from same, distal third of barb.
- Fig. 90. *Rhamphastus ariel*.
a. Distal barbule from back feather.
- Fig. 91. *Jacamerops grandis*.
a. Distal barbule from inner vane of remex.
b. Distal barbule from outer vane of remex.
c. Proximal barbule from same, distal third of barb.
- Fig. 92. *Cyanocitta stelleri*.
a. Distal barbule from inner vane of remex.
b. Proximal barbule from same.
c. Distal barbule from outer vane of remex.
d. Proximal barbule from same.
e. Distal barbule from breast feather.
f. Proximal barbule from same.
- Fig. 93. *Myiarchus cinerascens*.
a. Proximal barbule from outer vane of remex, distal half of barb.
- Fig. 94. *Pipilo maculatus*.
a. Distal barbule from inner vane of remex.
- Fig. 95. *Bombycilla garrula*.
a. Tip of covert feather, with "wax tip". \times 7.

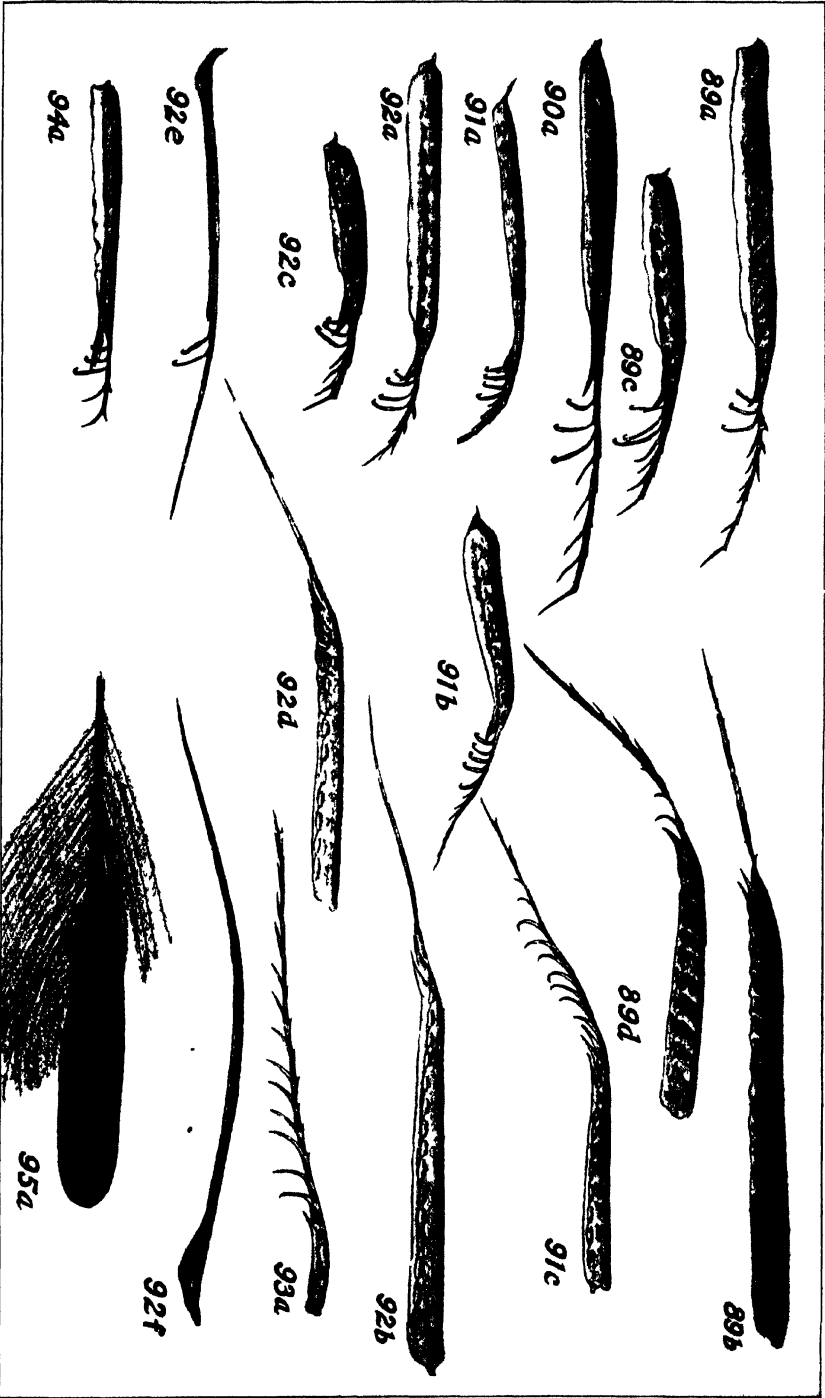


PLATE 34

TYPES OF DOWN BARBULES

Entire barbules drawn $\times 40$; portions of barbules marked in parenthesis drawn enlarged, $\times 285$.

Fig. 96. *Spheniscus mendiculus*.

a. Entire barbule. b. same, enlarged.

Fig. 97. *Puffinus griseus*.

a. Entire barbule. b. basal portion. c. terminal portion.

Fig. 98. *Sula variegata*.

a. Entire barbule. b. same, enlarged.

Fig. 99. *Plotus anhinga*.

a. Entire barbule. b. basal portion. c. terminal portion.

Fig. 100. *Botaurus lentiginosus*.

a. Entire barbule. b. basal portion. c. terminal portion.

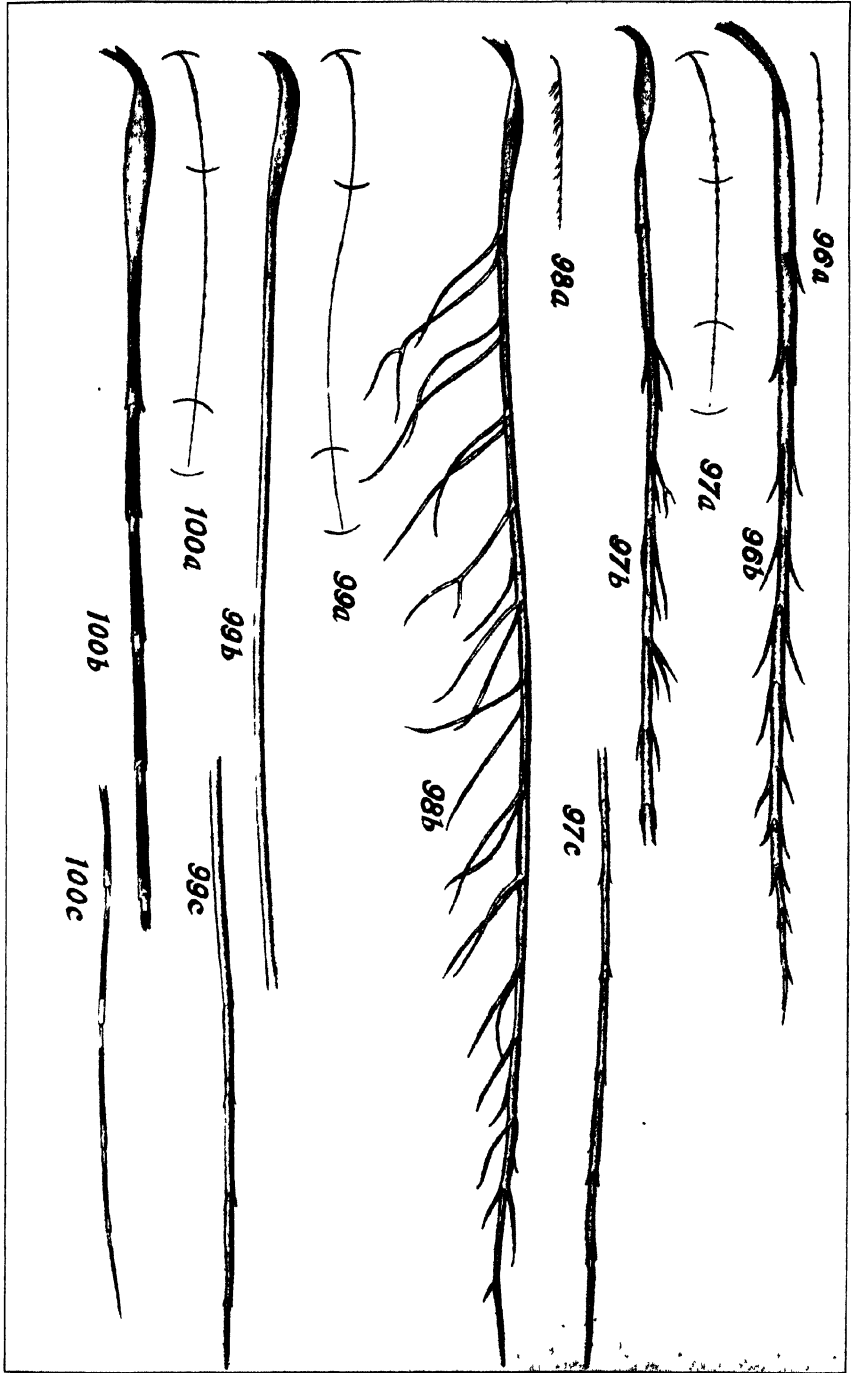


PLATE 35

TYPES OF DOWN BARBULES, *continued*

Entire barbules drawn $\times 40$; portions of barbules marked in parenthesis drawn enlarged, $\times 285$.

Fig. 101. *Guara rubra*.

a. Entire barbule. b. basal portion. c. terminal portion.

Fig. 102. *Phoenicopterus ruber*.

a. Entire barbule. b. basal portion. c. terminal portion.

Fig. 103. *Olor columbianus*.

a. Entire barbule. b. basal portion. c. terminal portion.

Fig. 104. *Mergus americanus*.

a. Entire barbule. b. basal portion. c. distal portion.

Fig. 105. *Falco sparverius*.

a. Entire barbule. b. basal portion. c. middle portion. d. terminal portion.

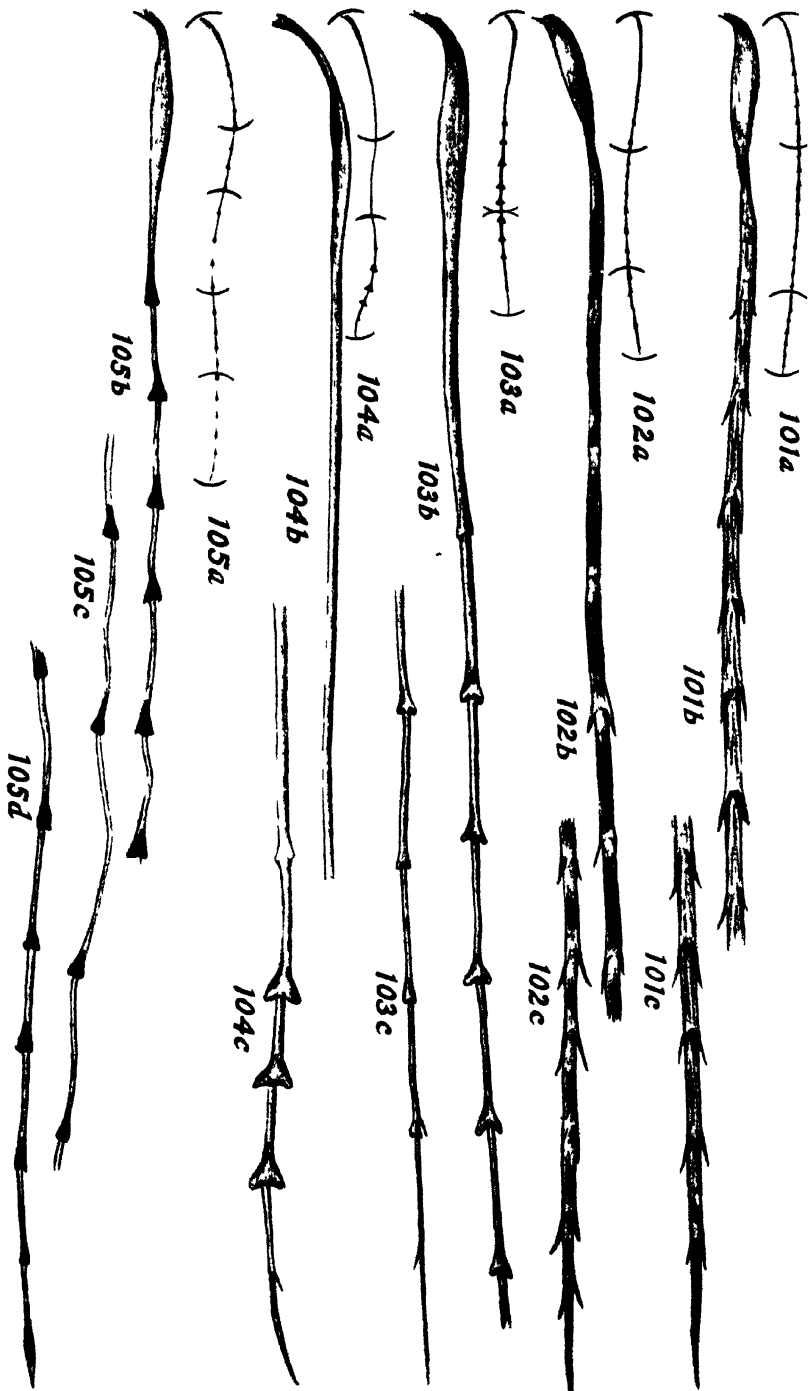


PLATE 36

TYPES OF DOWN BARBULES, *continued*

Entire barbules drawn $\times 40$; portions of barbules marked by parenthesis drawn enlarged, $\times 285$.

Fig. 106. *Eurypyga helas*.

a. Entire barbule. b. basal portion. c. terminal portion.

Fig. 107. *Rallus obsoletus*.

a. Entire barbule. b. basal portion. c. terminal portion.

Fig. 108. *Meleagris virginiana*.

a. Entire barbule from distal vanule near base of barb.

b. Basal portion. c. middle portion. d. terminal portion.

Fig. 109. *Zenaidura macroura*.

a. Entire barbule from near base of barb.

b. Basal portion. c. middle portion. d. terminal portion.

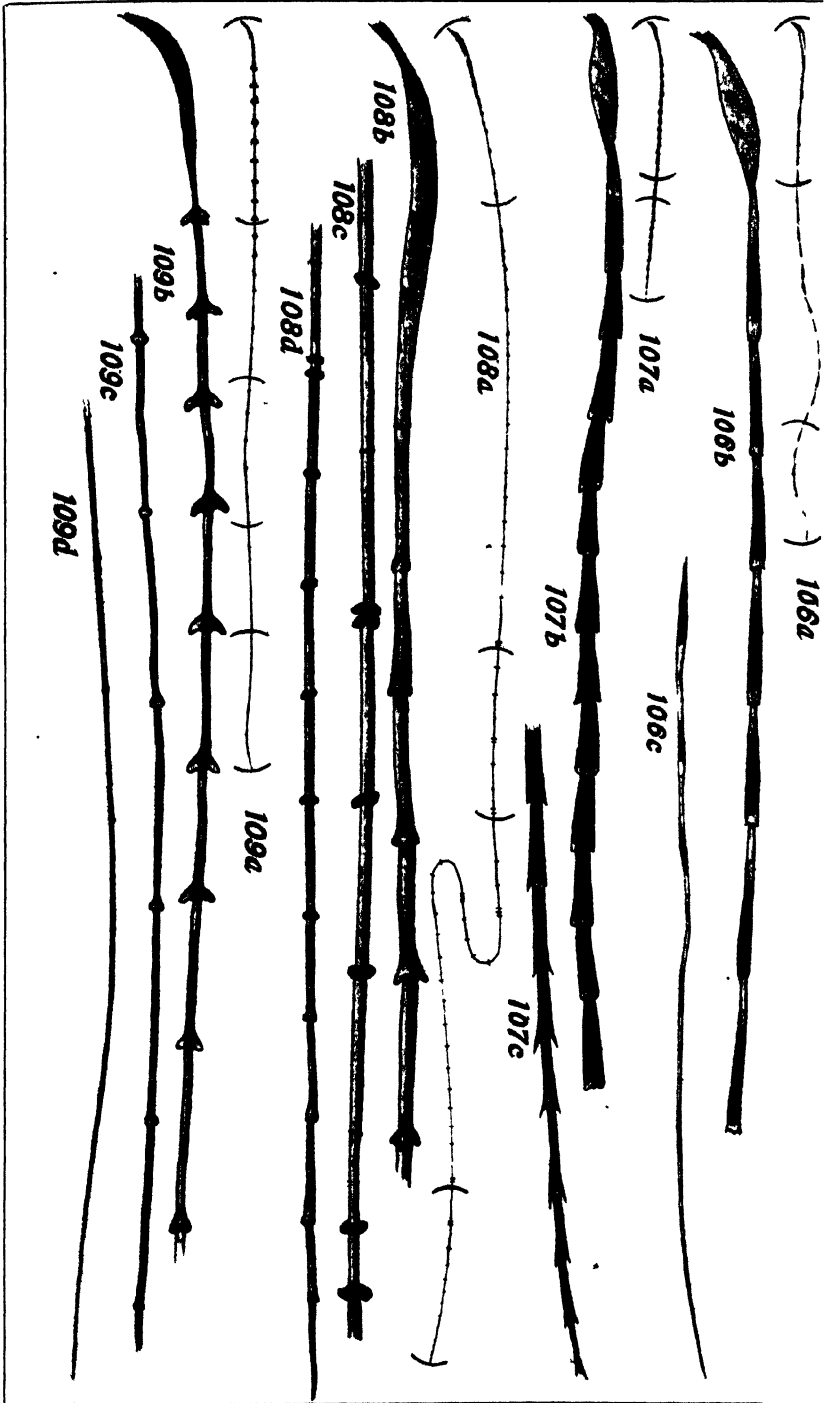


PLATE 37

TYPES OF DOWN BARBULES, *continued*

Entire barbules drawn $\times 40$; portions of barbules marked by parenthesis drawn enlarged, $\times 285$.

Fig. 110. *Momotus lessoni*.

a. Entire barbule. b. basal portion. c. terminal portion.

Fig. 111. *Hydrocorax mindanensis*.

a. Entire barbule. b. basal portion. c. terminal portion.

Fig. 112. *Eugenes fulgens*.

a. Entire barbule from near base of barb.

b. Basal portion. c. distal portion.

Fig. 113. *Rhamphastus ariel*.

a. Entire barbule from near base of barb.

b. Basal portion. c. terminal portion.

Fig. 114. *Pipilo maculatus*.

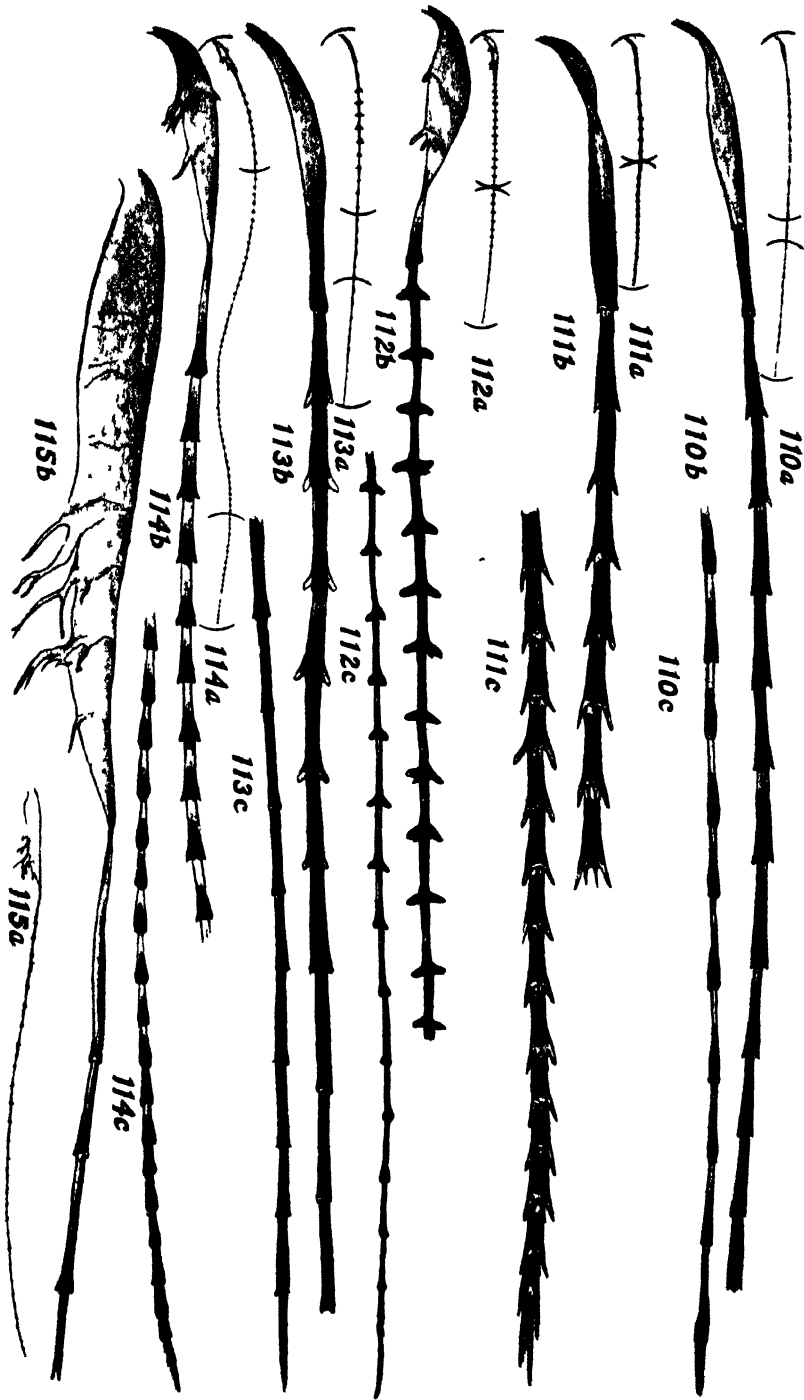
a. Entire barbule from near base of basal barb.

b. Basal portion. c. terminal portion.

Fig. 115. *Corvus corax*.

a. Entire barbule from near base of basal barb.

b. Basal portion.



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March 7, 1916

ANATOMICAL ADAPTATIONS IN THE
THORACIC LIMB OF THE CALIFORNIA POCKET
GOPHER AND OTHER RODENTS

BY
CHARLES DANIEL HOLLIGER

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INTRODUCTION

Structural adaptations are interesting, not only because of their close connection with problems of heredity and speciation, but also because they are the basis of the interest which inherently attaches to specialized forms. When we see a highly modified animal type we naturally look about to see what factors in the animal's environment have been responsible for the specialized developments in its morphology. Every such study of modified forms must necessarily be accompanied by comparison, since specialization is always a relative term.

It was with the idea of studying anatomical adaptation to habits

of life in some mammalian group that the work described herein was undertaken, over two years ago. There was no expectation that any new light could be thrown on the *cause* of specialization, but it seemed possible that, by carefully studying the *nature* of specialization in some type, a close correlation might be established between the habits and environment and the modified anatomy of the form.

In connection with the carrying out of this study, Professor J. Frank Daniel, of the University of California, has given constant advice and assistance, and has verified the greater part of the anatomical work. Professor C. A. Kofoed suggested the general line of study and the idea of quantitative comparison of structures. Professor J. C. Merriam has given indispensable advice on several questions of osteology. Many valuable suggestions and a large part of the material for study have been furnished by Dr. Joseph Grinnell and Mr. F. H. Holden of the California Museum of Vertebrate Zoology. To these persons the sincere thanks of the author are due.

CORRELATION OF ANATOMY WITH HABITS

SELECTION OF MATERIAL

The first step in the investigation was to find proper material upon which to study correlation between habits and anatomical structure. Several considerations had to be taken into account in selecting the group of mammals and the individual species to be studied: (1) The mammal for particular study should be highly differentiated from the primitive type; (2) its habits of life should be distinctive; (3) other members of the same group should be numerous; (4) material should be plentiful enough for thorough verification.

The California pocket gopher, *Thomomys bottae* (Eydoux et Gervais), seemed to meet all the above requirements to a greater extent than any other form available. The pocket gopher is highly specialized; its habits are characteristic; there are many other rodent families, some of which are more generalized, while some are specialized along different lines; material is in all cases abundant. These facts make the gopher an ideal subject for a study in anatomical adaptation to habits of life.

The pocket gopher differs from the general rodent type in almost every particular, and a detailed study of every organ and system

would undoubtedly be profitable in connection with this investigation. But since so complete an anatomical study was impracticable, it was necessary to select the structures employed in some particular function for close examination. The structures selected are those which most markedly distinguish the gopher from other rodents, namely, those associated with its fossorial, or underground, habit of life. The parts affected to the greatest extent by this mode of life are those connected with digging in the ground—namely, the bones and muscles of the anterior limb. A correlation of the fossorial habits of the gopher with the specialization in the anatomy of the thoracic limb is therefore the particular subject of the present study.

As material for comparison with the gopher, numerous rodents were available. The California ground squirrel (*Citellus beecheyi*) was selected because it belongs to one of the most primitive rodent groups living at the present time. The brown rat (*Epimys norvegicus*) was chosen because it is also a primitive form, and one little known anatomically, though the animal is so common. As a typical cursorial or surface-dwelling type of rodent, the Sacramento Valley cottontail (*Sylvilagus auduboni*) was first used. Later some specimens of the California jack rabbit (*Lepus californicus*), which is undoubtedly one of the most specialized of the rabbits, were secured. The Belgian hare (*Lepus europaeus*) was also employed in the earlier stages of the work. The anatomy of the hare is of interest chiefly in showing the effects of domestication on a specialized form. The Sierra chickaree or red squirrel (*Sciurus douglasi albolimbatus*) was taken as the type of arboreal or tree-dwelling rodent. The list of material studied thus includes rodents which have become adapted to the three principal modes of mammalian life, namely, fossorial, cursorial, and arboreal.

HABITS OF THE RODENTS STUDIED

The gopher passes practically its entire life underground. It seldom comes to the surface, and still more rarely quits its burrow entirely. It digs long tunnels several inches below the surface of the ground, occasionally making an opening for the purpose of pushing out the dirt. Actual digging is accomplished by means of powerful downward and backward strokes of the front feet. The strokes are made alternately with the right and the left foot,

and are so rapid that a continuous buzzing sound may sometimes be heard when the animal is working in hard ground. Three of the claws are extremely long and heavy, but in the species studied (*Thomomys bottae*) digits one and five are shorter and have blunt claws. The sides of the fingers are provided with long, stiff bristles which prevent dirt from passing between them; the hand is thus a broad scoop when the digits are separated. The loose earth is passed backward under the body by the fore feet, and the hind feet push it still farther back. C. H. Merriam (1895, p. 16) states that digging is aided by the long upper incisors, which are used as a pick in loosening hard earth; he also states that in pushing out loose earth at the surface the front feet are placed together under the chin, with the hands held vertically, the animal pushing itself forward with its hind feet until the earth is discharged from the opening of the tunnel. Stephens (1904, p. 142) states that in pushing out the loose earth the toes are "turned outward"; this is in line with our own observations made on a live gopher kept in a large glass jar half filled with earth.

With regard to the habits of the rodents used for purposes of comparison, only a few words are necessary. The ground squirrel lives largely underground and does considerable digging, but it prefers to appropriate and inhabit burrows made by other animals. The brown rat digs only occasionally when necessary to reach food or safety. The rabbits, as stated above, are primarily surface-dwelling forms and do little if any digging. Domesticated rabbits and hares, however, often make burrows in the breeding season. The chickaree is a tree-living form, spending but a small part of its time on the ground.

PLAN OF THE WORK

The bones of the thoracic limb of the pocket gopher were first studied in detail, and drawings were made of the whole skeleton of the leg, and of each part separately. The muscles of the thoracic region were then worked out. This was the more difficult because there are a number of modifications and changes from the arrangements of muscles found in mammals whose myology has been most studied, and because no description of the muscles of the foreleg of the gopher has been found in the literature. Drawings were then made of the muscles of the shoulder and foreleg of the gopher,

and also figures to show the origins and insertions of the muscles after these had been verified.

The next step was to compare the bones and muscles of the gopher with homologous structures in the other forms. In order to make these comparisons as definite as possible the quantitative method, explained later, was adopted. With the figures provided by these measurements it was then possible to draw certain conclusions bearing upon the principal subject under investigation, namely, the correlation or lack of correlation between anatomical specialization and habits of life.

OSTEOLOGY

The bones of the gopher with which this study is chiefly concerned are those forming the shoulder girdle, and the skeleton of the thoracic limb. While some of the muscles which furnish motive power to the limb originate on the skull, on the vertebrae, on the sternum, and on the ribs, as described in the discussion of muscles, it is outside our province to study in detail all of the above-named bony structures. Moreover, the bones of the foreleg exhibit most strongly the modifications correlated with the fossorial habits of the gopher.

The most noticeable general characteristic of the bones of the anterior leg of the gopher is their irregularity of outline. The various processes for muscular attachment, such as the spine of the scapula, the deltoid tuberosity and the condyles of the humerus, the olecranon of the ulna, and the pisiform bone of the carpus, are very noticeably larger in the gopher than in any of the other rodent forms dissected. If, as is probably true, we may infer the strength of a given muscle, or set of muscles, from the size of the bony tuberosity to which it is attached, we may say at once that the gopher has more powerful muscles in proportion to its size than any of the other species of rodents studied. Next to the gopher in irregularity of bones is the brown rat and then the ground squirrel. Thus the digging rodents have the most irregularly shaped bones, and by inference the most powerful muscles. The bones of the rabbits are the smoothest. If the relative length of the olecranon process in the different forms be taken as an index of the irregularity of the bones in general, we find (see table 2, p. 487) that the gopher stands at the head, and the jack rabbit at the bottom of the list of rodents studied.

Another general character of the skeleton which may be examined is the volume of the bones compared with the entire volume of the leg. Since greater volume may mean greater strength of the entire osseo-muscular machine, we might expect to find the fossorial members of the group again in the lead. But this seems not to be the case; table 1 (p. 485) indicates very little correlation between habits and volume of bones. Curiously enough, the bones of the jack rabbit are relatively larger than those of any of the other rodents. This is probably influenced by three factors: (1) The bones of the rabbits are thin-walled and therefore need to be relatively large; (2) The greater relative length of the limb in the rabbits increases the proportional volume of the bones; (3) The larger and broader foot also causes the skeleton to measure larger, since the whole foot was left attached to the leg skeleton when volumetric measurements were made. It thus seems that so many other factors besides habit of life influence the size of bones that any correlation with habit which might exist is hidden or obliterated.

The individual bones of the thoracic limb of the gopher will be described briefly, and important differences between the bones of this rodent and those of others of the series studied will be noted. The figures representing the bones are drawn to scale and no measurements are necessary.

Clavicle (fig. E).—In the gopher the clavicle is well developed and forms a true bony link between the sternum and the scapula. The head of the clavicle is a large, hemispherical knob, the mesial concave surface of which articulates with the cephalo-lateral angle of the manubrium of the sternum. The inner third of the shaft is

Fig. A. Lateral view of skeleton of left thoracic limb of the gopher, $\times 2$.

Fig. B. Mesial view of skeleton of left thoracic limb of the gopher, $\times 2$.

acr.—acromion

car.—carpus

cor. bd.—coracoid border.

cor. proc.—coracoid process

crvt. ang.—coracovertebral angle

del. tub.—deltoid tuberosity

ex. con.—external condyle

fal.—falciform

glen. ang.—glenoid angle

glen. bd.—glenoid border

glvt. ang.—glenovertebral angle

gr. tub.—greater tuberosity

hd.—head

hum.—humerus

in. con.—internal condyle

lat. gv.—lateral groove

les. tub.—lesser tuberosity

met.—metacarpals

nk.—neck

olec.—olecranon

ph.—phalanges

rad.—radius

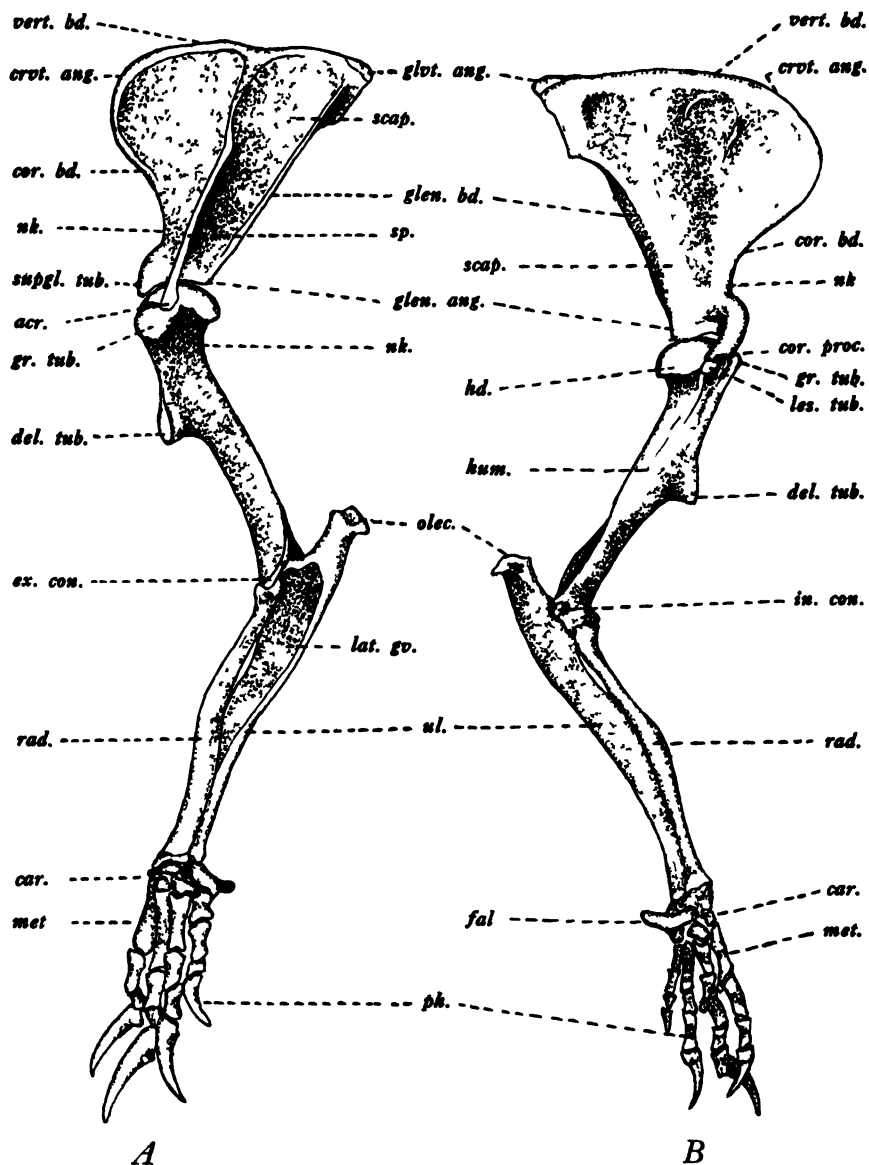
scap.—scapula

sp.—spine

supgl. tub.—supraglenoid tubercle

ul.—ulna

vert. bd.—vertebral border



rounded and straight. The lateral two-thirds is flattened dorso-ventrally, and curved slightly with the convexity cephalad. The lateral extremity of the clavicle is pointed, and articulates with the acromion of the scapula.

In the rabbits the clavicle is very small, reaching only about half the distance between the sternum and the acromion of the

scapula. In the squirrels and rat it is complete, that is, it forms a bony link between these two points.

The *scapula* (figs. C, D) may be described roughly as a triangular plate of bone with a high ridge, the spinous process, on its lateral surface. The flat, triangular plate is longest in the dorso-ventral direction, and its thickened ventral angle may be called the head of the bone. The distal surface of the head forms the concave glenoid fossa, in which the head of the humerus articulates. The coracoid process arises at the cephalic border of the glenoid fossa, and curves mesiad and ventrad. Its tip is in close relation with the lesser tuberosity of the humerus. The cephalic border of the

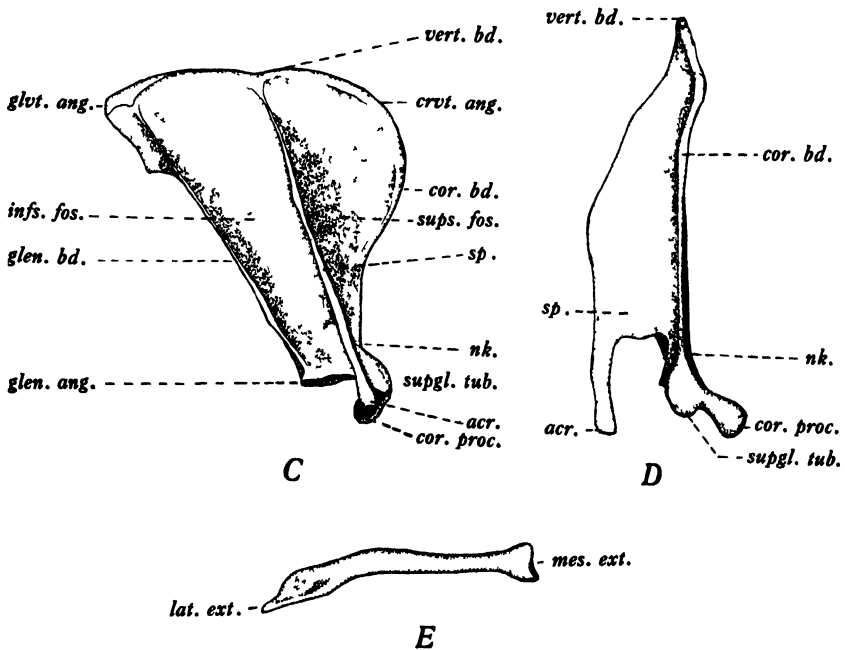


Fig. C. Lateral view of right scapula of the gopher, $\times 2\frac{3}{4}$

Fig. D. Anterior view of right scapula of the gopher, $\times 2\frac{3}{4}$

Fig. E. Ventral view of right clavicle of the gopher, $\times 2\frac{3}{4}$

acr.—acromion

cor. bd.—coracoid border

cor. proc.—coracoid process

crvt. ang.—coracovertebral angle

glen. ang.—glenoid angle

glen. bd.—glenoid border

glvt. ang.—glenovertebral angle

infs. fos.—infraspinous fossa

lat. ext.—lateral extremity

mes. ext.—mesial extremity

nk.—neck

sp.—spine

supgl. tub.—supraglenoid tubercle

sups. fos.—supraspinous fossa

vert. bd.—vertebral border

scapula may be called the coracoid, and the caudal the glenoid border. The coraco-vertebral angle is well rounded, while the gleno-vertebral angle is acute. The flat, central part of the bone is very thin in places, but a thickened border extends all around its edges. The spine arises along the long axis of the bone, dividing its lateral surface into two concave areas, the supraspinous and the infraspinous fossae. The mesial surface of the scapula is divided into three concave areas by two longitudinal ridges which correspond to the two concavities on the lateral surface (fig. B). These ridges

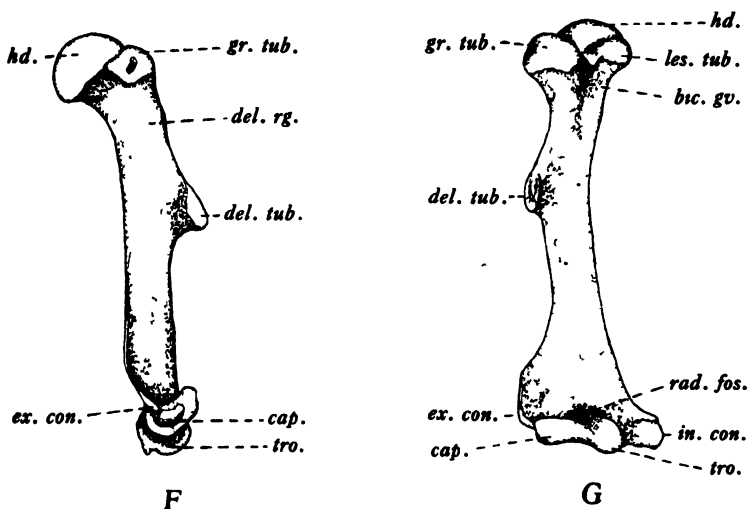


Fig. F. Lateral view of right humerus of the gopher, $\times 2\frac{3}{4}$

Fig. G. Anterior view of right humerus of the gopher, $\times 2\frac{3}{4}$

bic. gr.—bicipital groove

cap.—capitellum

del. rg.—deltoid ridge

del. tub.—deltoid tuberosity

ex. con.—external condyle

gr. tub.—greater tuberosity

hd.—head

in. con.—internal condyle

les. tub.—lesser tuberosity

rad. fos.—radial fossa

tro.—trochlea

strengthen the bone, and provide additional surface for the attachment of the subscapularis muscle. The spinous process is very high (*sp.*, fig. D). It gradually increases in height from the vertebral border, and reaches its highest point about the middle of the length of the bone. The base of the spine extends down to the neck, while the acromion process reaches nearly as low as the tip of the coracoid process. The end of the acromion is in close relation with the greater tuberosity of the humerus. No metacromion is apparent in the gopher.

The scapula in the rabbits, the squirrels and the rat is relatively longer and more slender than in the gopher, and the coracoid process is short, especially in the rabbits. The spinous process, however, shows most variation in the different types. In the rabbits the spine is low and its caudal surface is concave. It ends in a short acromion, while the metacromion forms a long process extending backward from the acromion at right angles to the spine. In the squirrels the acromion is the longer process, and curves cephalad from the tip of the spine. In the rat the end of the spine is flattened laterally and the acromion and metacromion are not distinct.

The *humerus* (figs. F, G) in the gopher is a short, irregular bone with enlarged extremities and a high process near the middle of the cephalo-lateral border. The proximal extremity is composed of three enlargements; the head, the greater tuberosity laterad, and the lesser tuberosity mesiad. Between the two tuberosities on the cephalic surface is the bicipital groove. The shaft just distal to the head is triangular, with its sharpest angle, formed by the deltoid ridge, cephalo-laterad. The deltoid ridge begins at the base of the greater tuberosity and increases rapidly in height until about the middle of the bone, where it forms the high deltoid tuberosity. This tuberosity is one of the characteristics of the humerus of the gopher; it is as high as the whole diameter of the bone just distal to it (fig. F). Just below this point the bone is flattened laterally, but it rapidly broadens out so that it becomes flat antero-posteriorly, spreading to form the high condyles. The external supracondylar ridge is high and sharp; the internal supracondylar ridge is low and rounded, but this condyle is much higher than the external. The articular surface occupies about two-thirds of the width of the distal end of the bone. This articulation is an excellent example of a hinge joint without any lateral motion. Examination of the bones shows that the forearm is incapable of being set in a straight line with the upper arm; at the greatest extension the bones form an angle of about 135° .

Of the other types examined the humerus of the rat most nearly resembles that of the gopher. It is irregular in the former, but relatively more slender than in the gopher. The humeri of the two squirrels are much alike in shape, with the deltoid tuberosities low and rounded, and the external supracondylar ridges remarkably long and high. The humerus of the ground squirrel is proportion-

ally much heavier than that of the tree squirrel. In the rabbits the humerus is smooth and round, with a very large head for articulation with the glenoid cavity of the scapula. The deltoid tuberosity is hardly noticeable in the rabbits. The humerus is relatively heaviest among the rabbits in the Belgian hare.

The *ulna* (*ul.*, figs. H, I) in the gopher is flattened laterally in its proximal three-fourths and rounded in its distal fourth. The

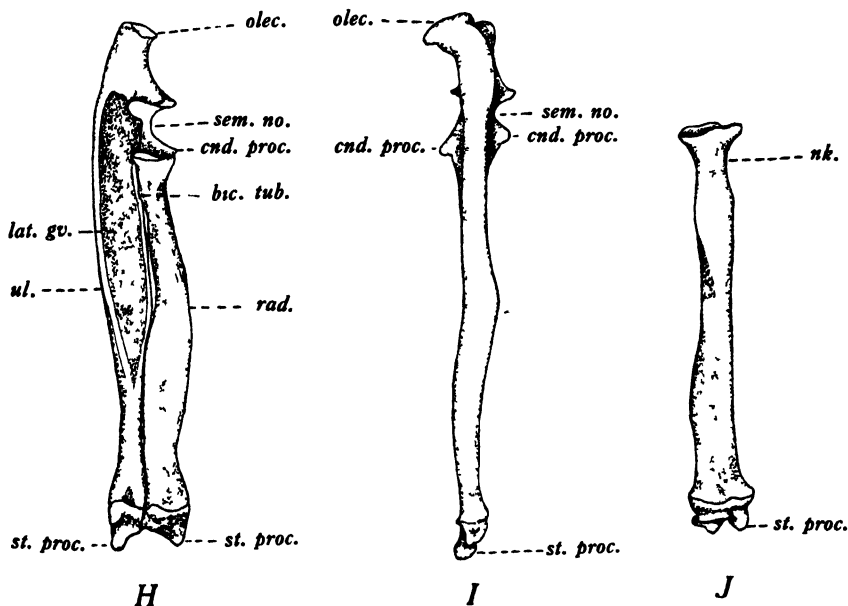


Fig H. Lateral view of right ulna and radius of the gopher, $\times 2\frac{3}{4}$

Fig I. Posterior view of right ulna of the gopher, $\times 2\frac{3}{4}$

Fig. J. Anterior view of right radius of the gopher, $\times 2\frac{3}{4}$

bic. tub.—bicipital tuberosity

cnd. proc.—coronoid process

lat. gv.—lateral groove

nk.—neck

olec.—olecranon

rad.—radius

sem. no.—semilunar notch

st. proc.—styloid process

ul.—ulna

sigmoid notch occupies the cephalic surface one-fourth the length of the bone from its proximal extremity; it is bounded by the lip of the olecranon process proximally and by the coronoid process distally. These processes are broad, and higher mesially than laterally. The olecranon process is very long and heavy, and a sharp projection at the mesial side of its tip (fig. I) greatly increases the surface for muscular attachment. The lateral surface

of the shaft of the bone is deeply grooved from the base of the olecranon process to the junction of the middle and distal thirds. The ulna ends in an enlarged head bearing the long, sharp styloid process which articulates with the cuneiform bone (*st. proc.*, figs. H, I).

The ulna in the various rodents examined is typical of the whole skeleton of the limb—long and slender and curved dorso-ventrad in the rabbits, relatively heavier in the tree squirrel, and still heavier and more irregular in the ground squirrel and rat. The most marked difference, however, is in the length of the olecranon process. This difference is so significant that it is taken up later in detail (see p. 487).

The *radius* (*rad.*, figs. H, J) is a fairly stout bone, three-fourths the length of the ulna, and curved slightly with its convexity cephalad. Its head is enlarged and bears an oval articular surface which rests against the capitellum of the humerus. Distad of the head the shaft is flattened dorso-ventrally for its upper third. The distal two-thirds of the bone is somewhat angular, and increases in diameter toward the extremity; this bears the sharp styloid process mesially, and the articular surface for the scapholunar laterally. Little rotary movement is provided for in the radius of the gopher, as is shown by the very close attachment of the radius and ulna in their distal half, and by the oval (not circular) proximal articular surface of the radius. However, a slight amount of supination and pronation is shown, even in the alcohol-hardened ligamentary skeleton.

The radius in the rabbits is much stronger than the ulna. In the squirrels the bones are of about equal strength, while in the rat and gopher the ulna is stronger, particularly in its proximal half. The radius and ulna of the rabbits are very closely bound together throughout their whole length, and probably permit of no rotation whatever. In the tree squirrel the interosseous ligament is broad, and the degree of rotation is undoubtedly greater than in any of the other forms. Another evidence of this difference between the rabbit and tree squirrel is the fact that in the squirrel the bones of the forearm are practically straight, while in the rabbits they are much curved.

A remarkable structure connected with the skeleton of the anterior leg of the gopher is the greatly enlarged and elongated external collateral or lateral humero-ulnar ligament. In man, in

the carnivora, and in most rodents this ligament is only a strengthening part of the capsular ligament of the joint, and is scarcely noticeable as a separate structure. In the gopher, however, it forms a heavy band of fibrous connective tissue extending from the lateral condyle of the humerus to the middle of the dorso-lateral border of the ulna (*lig.*, fig. S). It thus bridges over the deeply grooved external surface of the ulna, and over the abductor

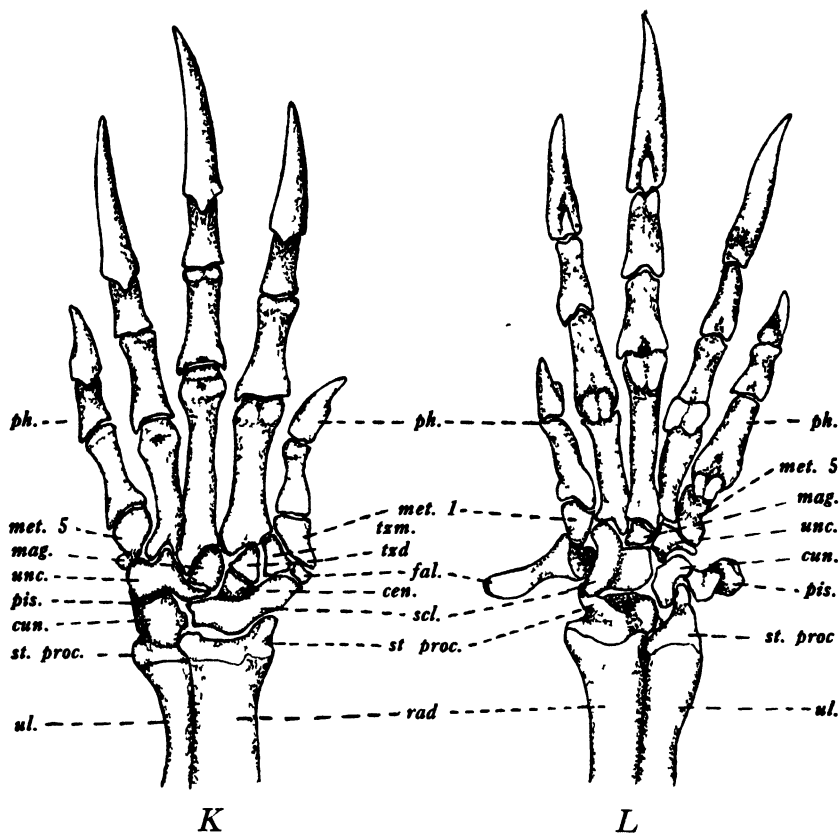


Fig. K. Dorsal view of skeleton of left manus of the gopher, $\times 4$

Fig. L. Palmar view of skeleton of left manus of the gopher, $\times 4$.

cen.—centrale

cun.—cuneiform

fal.—falciform (deflected in fig. L)

mag.—magnum

met.—metacarpals

met. 1—metacarpal 1

met. 5—metacarpal 5

ph.—phalanges

pis.—pisiform (deflected in fig. L)

rad—radius

scl.—scapholunar

st. proc.—styloid process

tzd.—trapezoid

tzm.—trapezium

ul.—ulna

unc.—unciform

pollicis longus muscle which occupies this groove (see p. 478). Contrary to what might be expected, the nearest approach to this structure in any of the rodents examined is found in the jack rabbit, the animal otherwise most widely different from the gopher. In the jack rabbit, and to a lesser extent in the cottontail, a strong ligament connects the lateral condyle of the humerus with the ventro-lateral border of the ulna. It does not, however, bridge over any muscle, and its length is only about one-ninth that of the ulna, while in the gopher it is nearly one-half as long as the ulna.

A probable explanation of the existence of this ligament in the gopher is the fact that the flexor muscles of the manus are much stronger than the extensors. Being attached to the high mesial condyle of the humerus, the flexors would tend to adduct the forearm were this effect not counteracted by a very strong lateral humero-ulnar ligament.

The *carpus* (figs. K, L) in the gopher is composed of nine bones. Three of these form the proximal row—the scapholunar, cuneiform, and pisiform—and six the distal row—the falciform, trapezium, trapezoid, centrale, magnum, and unciform. Of these six the centrale and pisiform articulate only with other bones of the carpus; all the other members are in relation either with the bones of the forearm or with the metacarpals. The pisiform and falciform are generally considered to be developed as sesamoid bones. The following brief descriptions should be supplemented by reference to the figures and it should be remembered that here, as in most quadrupeds, the radius is the mesial and the ulna the lateral bone in the distal part of the forearm.

The scapholunar is the largest of the carpal bones, and articulates proximally with the radius, distally with all the bones of the second row, and on the lateral (ulnar) side with the cuneiform. The cuneiform lies between the ulna and the unciform, and supports the pisiform on its palmar surface. The pisiform is very large in the gopher (*pis.*, fig. L) and projects out at right angles to the surface of the carpus. The unciform is an irregular bone supporting the bases of the fifth, fourth, and part of the base of the third metacarpal. The magnum is small and articulates with parts of the bases of the third and second metacarpals. The centrale is a tiny wedge of bone seen only on the dorsal surface. The trapezoid and trapezium are also small and do not appear on the palmar view of the carpus; the former articulates with a part of

the base of metacarpal 2, and the latter with the remainder of the base of this metacarpal, with the base of metacarpal 1, and proximally with the falciform bone. The falciform is a long, curved bone, its base tightly wedged in on the radial side of the carpus, and its body curving around until it meets the pisiform, to which it is bound by ligaments. There is thus formed on the palmar side of the carpus a strong, bony arch composed of the falciform and pisiform bones. Under this arch pass the tendons of the flexor muscles of the hand, and on it is inserted the flexor carpi ulnaris, the strongest muscle of the forearm (see p. 479).

In the carpus of the rabbits the falciform bone is absent, but the pisiform is very long and heavy. In the chickaree the arrangement is similar to that in the gopher, except that the falciform bone is small or absent. Hoffmann and Weyenbergh (1870, p. 27) in their description of the carpus of *Sciurus vulgaris* fail to mention the falciform bone; it is undoubtedly present, however, in *Sciurus d. albolimbatus*. In the ground squirrel the falciform is almost as well developed as in the gopher. The rat also possesses a long falciform bone.

Metacarpals (figs. K, L). The first metacarpal in the gopher is a short, triangular bone; the fifth metacarpal is also short and irregular. The smallness of these two bones has much to do with the shortness of digits 1 and 5. The three middle metacarpals are long and heavy, especially the third, which is the longest and stoutest. The bases of the metacarpals are irregular, and tightly wedged in among the carpal bones. Sesamoid bones occupy the palmar sides of the metacarpo-phalangeal articulations.

In the rabbits the four lateral metacarpals are long, rounded, rod-like bones, while the first is small and triangular. The lateral four metacarpals in the squirrels are also fairly even in length, while the first is extremely small. In the rat the metacarpals are considerably like those in the gopher, but are more slender.

Phalanges (ph., figs. K, L). The five digits in the gopher vary somewhat regularly in length from the long middle one to the short first and fifth. This variation is due partly to the metacarpals, as described above, and partly to the phalanges. The latter are longest and strongest in the middle digit and shortest in the outside fingers. Since the first digit, or thumb, has only two phalanges, it is about a third shorter than digit 5. The bones of the terminal phalanges or claws of the gopher are long and curved;

in the middle finger the skeleton of the claw is as long as the two proximal phalanges together. In life these terminal phalanges are covered by the sharp, horny claws, which increase their length considerably. Sesamoid bones are found on the palmar surface of the distal phalangeal joints.

The phalanges of the rabbits are short and slender and the claws are blunt. The squirrels have well developed phalanges except in the first digit, which is only about one-sixth as long as the third. The claws of the chickaree are long, curved, and sharp. The manus of the rat is relatively smaller than that of the gopher, and the claws are much shorter; digit 1 is shorter and digit 5 longer than corresponding members in the gopher.

MYOLOGY

The arrangement of the muscles of the anterior limb of the gopher resembles to a considerable extent that found in the rabbit, though several important differences will be noted in their proper places. In certain respects the musculature of the gopher is more like that of the ground squirrel or rat than like that of the rabbit, but since the latter animal is the rodent type most frequently used in laboratory study, our comparisons will usually be based on the muscular structure of the rabbit. At the same time, instances of close resemblance to other of the forms studied in this connection will be noted.

Cheek-Pouch Muscles.—The cheek pouches of the gopher are at least as highly developed as those of any other rodent, and while the musculature of these pouches has no connection with that of the anterior limb, it is interesting enough to merit a few words of description. Figure M shows the arrangement of these structures. The cheek pouches are sacs of skin lined with soft, short hairs; they extend from the angles of the mouth back to the shoulder where they cover the deltoid muscles. They are suspended along the sides of the cheek by fascia and muscle fibers, the latter having been described under the following names (Merriam, 1895, p. 101): The *protractor* of the pouch comprises fibers arising from the fascia of the *masseter* muscle; these fibers pass ventrad and caudad and spread out over the mesial and lateral surfaces of the pouch. Their contraction draws the posterior end of the pouch forward and assists in emptying it. The *levator* of the pouch arises along the caudal half of the nuchal ligament and passes laterad and

cephalad to be inserted in the dorso-caudal angle of the pouch. The function of this muscle is to support and elevate the rear end of the pouch. The *retractor* of the pouch is a long, band-like muscle which arises from the spinous processes of the last thoracic and first two lumbar vertebrae and the supraspinous ligament, and passes cephalad and ventrad over the shoulder, to be inserted into the whole of the caudal end of the pouch. Its action, as expressed by its name, is to retract the pouch. There is also a *ventral retractor* of the cheek pouch (not shown in fig. M). This arises from the manubrium of the sternum and passes laterad and cephalad, to be inserted on the caudo-ventral angle of the mesial wall of the pouch; its action is to draw the lower edge of the pouch mesiad beneath the chin. The opening of the cheek pouch, lying just laterad of the mouth opening, is surrounded by a *sphincter* muscle, which serves to close the mouth of the pouch. See Merriam (1895, pp. 17-19) and Stephens (1906, pp. 141, 142) for further descriptions of the structure and use of the cheek pouches of the pocket gopher.

Thoracic Limb Muscles.—The muscles of the thoracic limb proper will be taken up in the order in which they appear in the dissection. The plan usually followed in this work was to remove each muscle completely after it had been studied. The advantages of this method are as follows: (1) Origins and insertions can be traced more definitely than when the muscle must be saved for further study. (2) A much clearer view of deep muscles is obtained by removal of the superficial layers. (3) In measuring volumes of muscles, which will be discussed later, it was of course necessary to remove them completely.

The serial numbers preceding the following descriptions indicate the order in which the muscles may best be studied. These numbers will also be used occasionally in referring to muscles, and later in the grouping of muscles with a common function.

1. *Cutaneus maximus* (*cut. max.*, fig. M).—This is the first muscle encountered on removal of the skin, being very difficult to separate from the latter. It forms a thin sheet over the back, flanks and abdomen, arising from the subcutaneous fascia and joining with its fellow of the opposite side in the dorsal and ventral mid-lines. On the sides of the thorax the fibers converge to form a thick band which joins the pectoralis quartus and is inserted with it on the antero-mesial surface of the humerus just below the lesser



Fig. M.

Superficial muscles of the gopher, $\times 1$.

abd. aur.—abductor auris

cut. max.—cutaneous maximus

lev.—levator of pouch

lev. aur.—levator auris

prot.—protractor of pouch

retr.—retractor of pouch

sphin.—sphincter of pouch

tuberosity. Besides affording motion to the skin of the trunk, the cutaneous maximus in the gopher draws the leg backward and assists in digging movements. The cutaneous maximus is a prominent muscle in all the rodents examined, but it is especially well developed in the rat, in which it forms a very heavy layer beneath the skin of the caudal three-fourths of the trunk.

2. *Trapezius* (*trap.*, fig. N) is composed of three parts in the gopher; in the rabbit there are only two parts.

a. The cervical portion (*trap. a*, fig. P) arises from the mesial third of the lambdoid ridge of the skull, from the entire length of the nuchal ligament, and from the spines of the first, second and third thoracic vertebrae and the supraspinous ligament. The fibers pass laterad to be inserted along the whole length of the spine of the scapula and on the fascia of the acromio-clavicular articulation. This muscle is a thin, triangular layer, the function of which is to draw the scapula dorsad and to rotate its glenoid end forward. The rotating action of this and other muscles is explained by considering the scapula as pivoted on a horizontal axis through its center. Observation shows that much of its movement consists of rotation around such an axis.

b. The middle portion (*trap. b*, fig. P) of the trapezius arises from the spinous processes of the fifth and sixth thoracic vertebrae and the supraspinous ligament, and passes laterad and cephalad to be inserted with the thoracic portion.

c. The thoracic portion (*trap. c*, fig. P) arises from the spinous processes of the eleventh and twelfth thoracic and first lumbar vertebrae and the supraspinous ligament. It forms a narrow band of fibers which pass forward and, after being joined by the middle portion, are inserted on the proximal angle of the spine of the scapula. The action of parts *b* and *c* is to draw the scapula backward, and to rotate its glenoid end forward.

3. *Rhomboideus capitalis* (*rhom. cap.*, figs. P, S) lies immediately beneath 2a. This muscle in the gopher is unlike any muscle found in the other rodent forms studied. It resembles most nearly the *occipitoscapularis* of the cat (Reighard and Jennings, 1901, p. 118). C. H. Merriam (1895, p. 102) describes this muscle in the gopher under the name of the *rhomboideus*. The *rhomboideus capitalis* is a strong band of fibers which take origin along the lateral half of the lambdoid ridge of the skull, where the external half of the origin is overlapped by the origin of the cleidomastoid. It passes

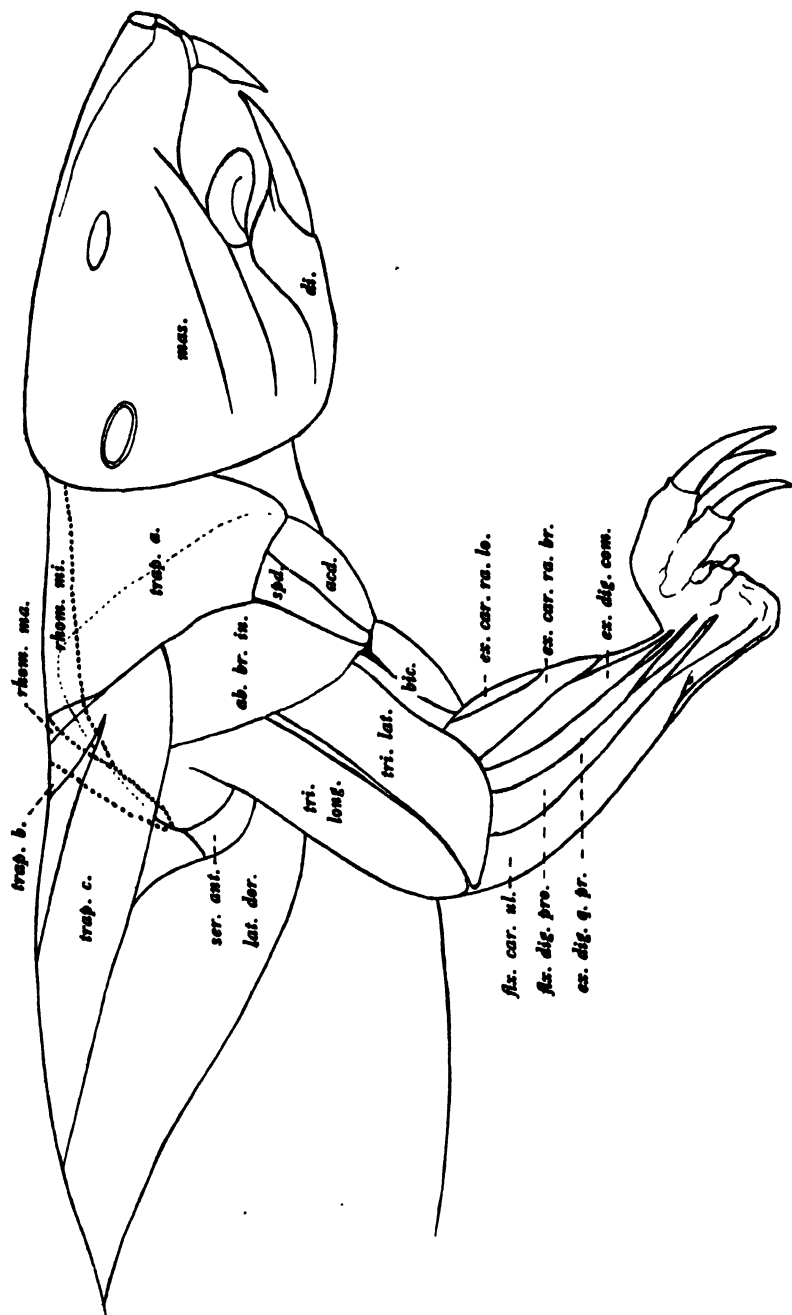


Fig. N. General view of thoracic limb muscles of the gopher after removal of the superficial muscles, $\times 1\frac{1}{2}$

<i>ab. br. in.</i> —abductor brachii inferior	<i>flx. dig. pro.</i> —flexor digitorum profundus
<i>acd.</i> —acromiodeltoideus	<i>lat. dor.</i> —latissimus dorsi
<i>bic.</i> —biceps brachii	<i>mas.</i> —masseter
<i>di.</i> —digastric	<i>rhom. ma.</i> —rhomboideus major
<i>ex. car. ra. br.</i> —extensor carpi radialis brevis	<i>rhom. mi.</i> —rhomboideus minor
<i>ex. car. ra. lo.</i> —extensor carpi radialis longus	<i>ser. ant.</i> —serratus anterior
<i>ex. dig. com.</i> —extensor digitorum communis	<i>spd.</i> —spinodeltoideus
<i>ex. dig. q. pr.</i> —extensor digiti quinti proprius	<i>trap. a.</i> —trapezius, cervical portion
<i>flx. car. ul.</i> —flexor carpi ulnaris	<i>trap. b.</i> —trapezius, middle portion
	<i>trap. c.</i> —trapezius, thoracic portion
	<i>tri. long.</i> —triceps, caput longum
	<i>tri. lat.</i> —triceps, caput laterale

caudad and is inserted on the cephalic half of the vertebral border and the dorsal two-thirds of the spine of the scapula. Its action draws the scapula forward and rotates the glenoid end backward. The origin of this muscle corresponds to the origin of the levator scapulae minor of the rabbit, and its insertion somewhat resembles the insertion of the levator scapulae major of the rabbit.

4. *Rhomboides minor* (*rhom. mi.*, figs. N, P). The two rhomboids are also exposed by removal of the trapezius; they are closely united and appear as one muscle in the gopher. The rhomboides minor arises on the nuchal ligament from the atlas to the spine of the second thoracic vertebra, and is inserted on the mesial surface of the cephalic two-thirds of the vertebral border of the scapula.

5. *Rhomboides major* (*rhom. ma.*, figs. N, P) arises from the spinous processes of the third and fourth thoracic vertebrae and the supraspinous ligament, and is inserted into the mesial surface of the caudal third of the vertebral border of the scapula. The action of both the rhomboids is to draw the scapula forward, and to rotate its glenoid end backward. The rhomboides major also draws the caudal angle dorsad.

6. *Latissimus dorsi* (*lat. dor.*, figs. N, P).—This muscle is found beneath the retractor of the cheek pouch and the middle and thoracic parts of the trapezius. It arises from the lumbar fascia, from the spinous processes of thoracic vertebrae from the sixth to the twelfth, inclusive, and from the supraspinous ligament. It passes as a flat, triangular sheet over the side of the thorax, and is inserted into the mesial side of the humerus just below the lesser

tuberosity (*lat. dor.*, pl. 39). Its tendon joins that of the *teres major* just before their common insertion. The *latissimus dorsi* is a strong adductor and flexor of the foreleg, and is well developed in the gopher where it helps to produce the downward and backward stroke of the arm in digging.

7. *Sternomastoideus* (*stm.*, fig. O).—This is primarily a muscle of the head, but may be considered briefly here. It arises from the manubrium of the sternum and the sterno-clavicular ligament, and is inserted on the lateral and caudal surfaces of the mastoid process of the skull. It draws the head downward and sidewise.

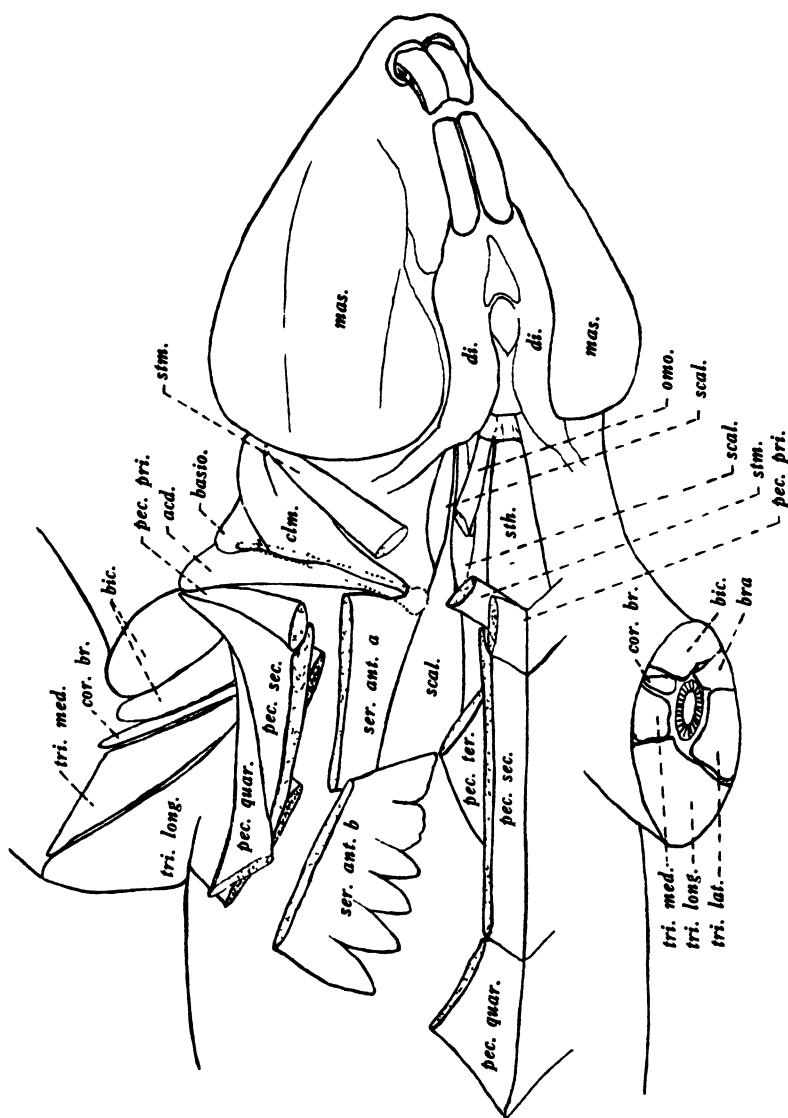
8. *Cleidomastoideus* (*clm.*, fig. O).—This muscle in the gopher is distinctly divided into two parts, as shown in the figure. Both parts arise on the dorsal surface of the mastoid process of the skull, the lateral part superficial to the mesial part. The insertion is on the cephalic surface of the clavicle, the lateral part occupying the outer third and the mesial part the inner two-thirds. The *cleidomastoideus* acts both on the head and on the shoulder girdle; the head is drawn downward and sidewise when the clavicle is fixed, and the shoulder is drawn forward and upward when the head is fixed.

9. *Basioclavicularis* (*basio.*, fig. S) arises on the ventral border of the transverse process of the atlas and passes laterad and caudad beneath the *sternomastoideus* and *cleidomastoideus* to be inserted on the anterior surface of the lateral fourth of the clavicle, and the cleido-humeral ligament. In the rabbit this muscle arises on the basioccipital and sphenoid bones of the skull. This muscle probably acts in both directions, drawing the head to the side or the shoulder forward, depending on which part is fixed.

Fig. O. Vento-lateral view of muscles of the neck and shoulder of the gopher, $\times 1\frac{1}{2}$

acd.—acromiodeltoideus
basio.—basioclavicularis
bic.—biceps brachii
bra.—brachialis
clm.—cleidomastoideus
cor. br.—coracobrachialis
di.—digastric
mas.—masseter
omo.—omohyoideus
pec. pri.—pectoralis primus
pec. quar.—pectoralis quartus
pec. sec.—pectoralis secundus

pec. ter.—pectoralis tertius
scal.—scalenus
ser. ant. a.—serratus anterior, cervical portion
ser. ant. b.—serratus anterior, thoracic portion
sth.—sternohyoideus
stm.—sternomastoideus
tri. long.—triceps, caput longum
tri. lat.—triceps, caput laterale
tri. med.—triceps, caput mediale



10. *Omohyoideus* (omo., fig. R).—While not present in the rabbit, this muscle is well developed in the gopher. It arises from the lateral part of the body of the hyoid bone, and passes caudad and laterad to be inserted in the cephalic border of the neck of the scapula, passing in between the supraspinatus and the subscapu-

laris. Its action on the shoulder girdle is similar to that of the preceding three muscles.

11. *Pectoralis* (*pec.*, figs. O, P, R) is extremely well developed in the gopher; as in the rabbit, it consists of four parts.

a. *Pectoralis primus* arises from the manubrium of the sternum and is inserted on the mesial surface of the distal part of the deltoid tuberosity of the humerus.

b. *Pectoralis secundus* arises along the lateral part of the sternum from the manubrium to the xiphoid cartilage; it is inserted on the humerus with 11a (*pec. sec.*, pl. 39).

c. *Pectoralis tertius* arises from the sternum and costal cartilages from the second to the fifth, inclusive. It is entirely covered by 11a and 11b, and the fibers pass more cephalad to be inserted on the mesial surface of the coracoid process of the scapula (*pec. ter.*, pl. 39).

d. *Pectoralis quartus* arises from the xiphoid cartilage of the sternum and the abdominal fascia; it passes forward and outward to be inserted in common with the cutaneus maximus on the mesial surface of the proximal part of the deltoid tuberosity (*pec. quar.*, pl. 39). It will be noted (fig. O) that these fibers pass beneath those of 11a and 11b, an arrangement resembling that found in the human *pectoralis major*.

The *pectoralis* of the gopher is an important muscle in digging. Its insertion is well down on the humerus, increasing the leverage of this muscle and rendering the downward and backward stroke of the arm more powerful.

12. *Subclavius* (*subcl.*, fig. R) is a small and unimportant muscle arising from the junction of the first rib with its costal cartilage, and inserted on the dorsal and caudal surfaces of the lateral half of the clavicle. It helps to hold the clavicle in place.

13. *Serratus anterior* (*ser. ant.*, fig. P). As in all quadrupeds, this muscle is important in suspending the body between the fore legs; the two *serrati* form a sling in which the thorax rests. In contracting they pull the scapula downward or the body upward, depending upon which is the fixed point. There are two parts to this muscle, between which the largest part of the scalenus passes (*scal.*, fig. O).

a. The cervical portion arises from the transverse processes of cervical vertebrae from the third to the seventh, inclusive, and from the first two ribs; it is inserted into the cephalic five-sixths

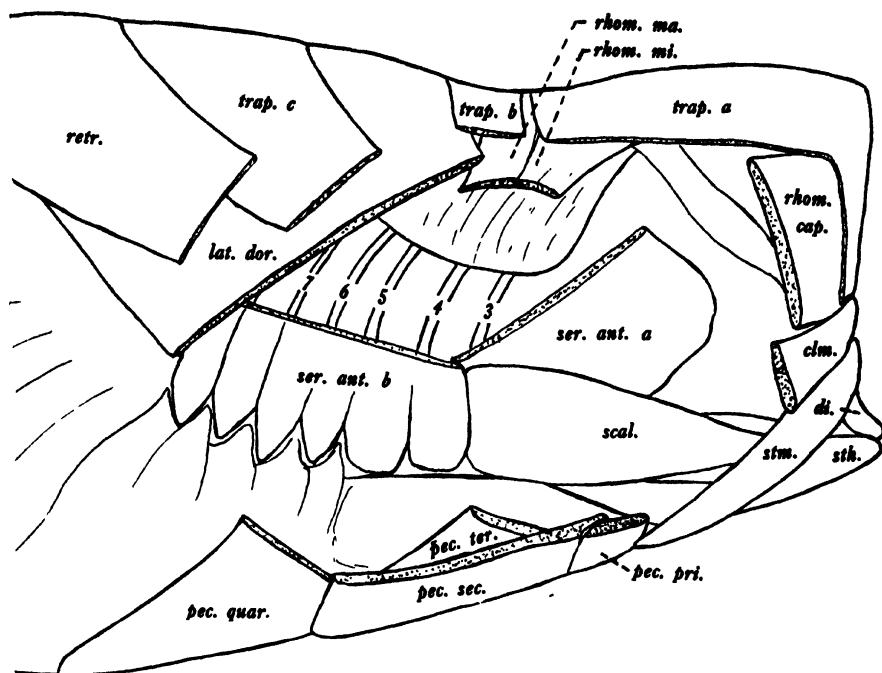


Fig. P. Lateral view of shoulder muscles of the gopher after removal of the leg, $\times 2$.

cim.—cleidomastoideus
di.—digastric
lat. dor.—latissimus dorsi
pec. pri.—pectoralis primus
pec. quar.—pectoralis quartus
pec. sec.—pectoralis secundus
pec. ter.—pectoralis tertius
retr.—retractor of pouch
rhom. cap.—rhomboideus capitalis
rhom. ma.—rhomboideus major
rhom. mi.—rhomboideus minor

scal.—scalenus
ser. ant. a.—serratus anterior, cervical portion
ser. ant. b.—serratus anterior, thoracic portion
sth.—sternohyoideus
stm.—sternomastoideus
trap. a.—trapezius, cervical portion
trap. b.—trapezius, middle portion
trap. c.—trapezius, thoracic portion
 3 4 5 6 7—ribs

of the mesial surface of the vertebral border of the scapula (*ser. ant. a*, pl. 39).

b. The thoracic portion arises from the third to the eighth ribs, inclusive, by separate slips (*ser. ant. b*, fig. P), and is inserted on the caudal one-sixth of the mesial side of the vertebral border of the scapula.

14. *Deltoideus* (*spd.*, *acd.*, fig. S) in the gopher is made up of two distinct parts:

a. *Acromiodeltoideus* arises from the outer three-fourths of the ventral surface of the clavicle and the tip of the acromion of

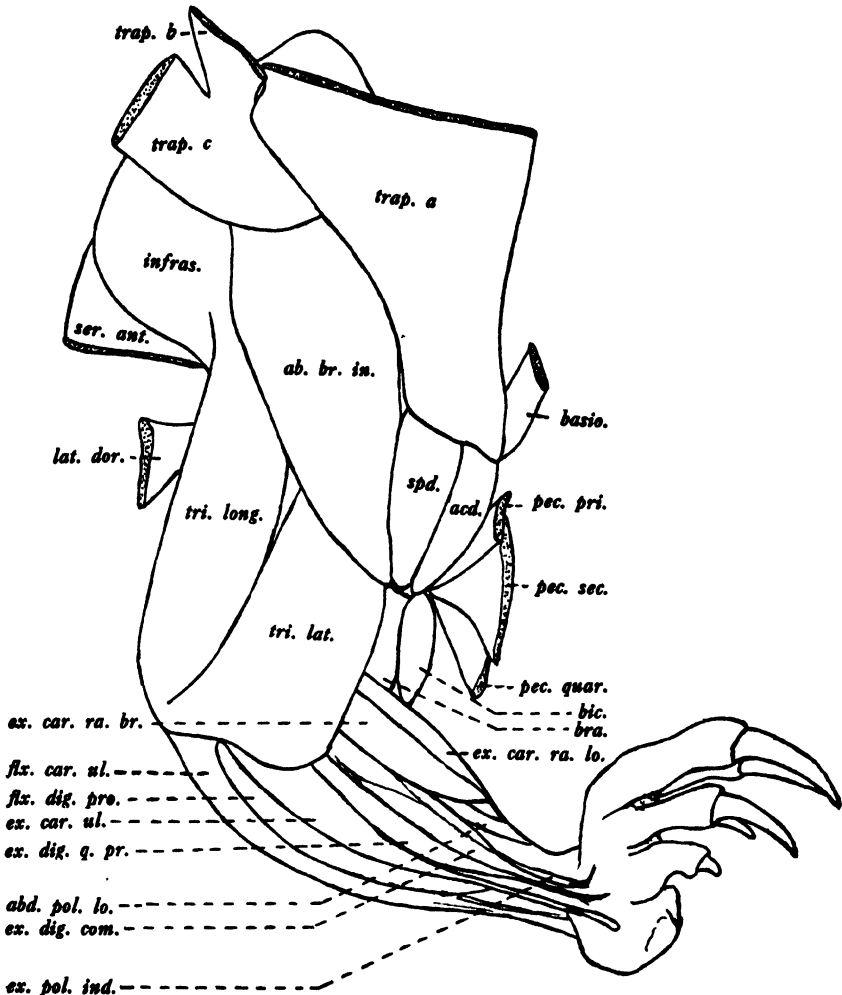


Fig. Q. Lateral view of superficial muscles of right thoracic limb of the gopher, $\times 2$.

ab. br. in.—abductor brachii inferior
 abd. pol. lo.—abductor pollicis longus
 acd.—acromiodeltoideus
 basio.—basioclavicularis
 bic.—biceps brachii
 bra.—brachialis
 ex. car. ra. br.—extensor carpi radi-
 alis brevis
 ex. car. ra. lo.—extensor carpi radi-
 alis longus
 ex. car. ul.—extensor carpi ulnaris
 ex. dig. com.—extensor digitorum
 communis
 ex. dig. q. pr.—extensor digiti quinti
 proprius
 ex. pol. ind.—extensor pollicis et in-
 ducis

flx. car. ul.—flexor carpi ulnaris
 flx. dig. pro.—flexor digitorum pro-
 fundus
 infras.—infraspinatus
 lat. dor.—latissimus dorsi
 pec. pri.—pectoralis primus
 pec. quar.—pectoralis quartus
 pec. sec.—pectoralis secundus
 ser. ant. a—serratus anterior, cervical
 portion
 spd.—spinodeltoideus
 trap. a—trapezius, cervical portion
 trap. b—trapezius, middle portion
 trap. c—trapezius, thoracic portion
 tri. long.—triceps, caput longum
 tri. lat.—triceps, caput laterale

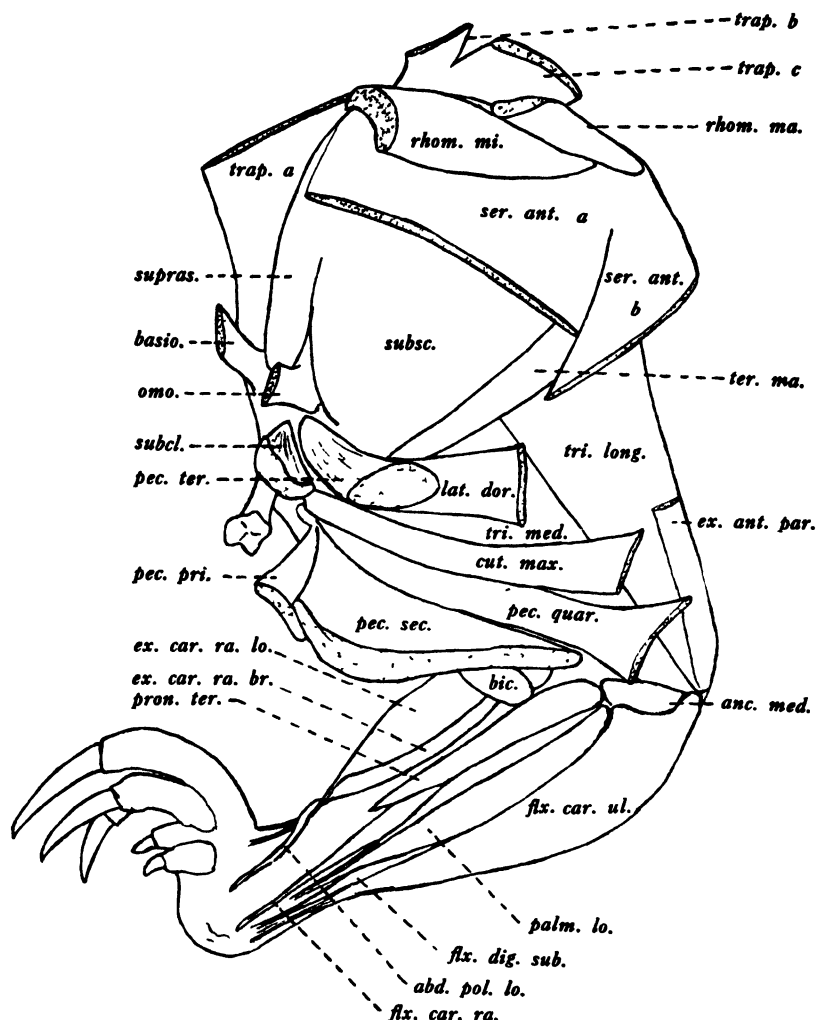


Fig. R. Mesial view of right thoracic limb of the gopher after removal from the body, $\times 2$.

anc. med.—anconeus medialis
cut. max.—cutaneus maximus
ex. ant. par.—extensor antibrachii parvus
flx. car. ra.—flexor carpi radialis
flx. dig. sub.—flexor digitorum sublimis
omo.—omohyoideus
palm. lo.—palmaris longus
pec. ter.—pectoralis tertius

pron. ter.—pronator teres
rhom. ma.—rhomboides major
rhom. mi.—rhomboides minor
ser. ant. b.—serratus anterior, thoracic portion
subcl.—subclavius
subsc.—subscapularis
supras.—supraspinatus
ter. ma.—teres major
tri. med.—triceps, caput mediale

For other abbreviations see explanation to Fig. Q.

the scapula; it is inserted into the lateral surface of the deltoid tuberosity of the humerus.

b. *Spinodeltoideus* arises from the spine and acromion of the scapula, and is inserted with 14a. The deltoids abduct and draw forward the humerus.

15. *Abductor brachii inferior* (*ab. br. in.*, fig. Q), corresponds to the scapular part of the deltoid in man. It is a thin sheet of muscle covering the infraspinatus; it arises on the spine of the scapula for almost its entire length, and from the fascia of the infraspinatus, and is inserted on the deltoid tuberosity with the deltoids. This muscle assists in flexing and abducting the humerus.

16. *Supraspinatus* (*supras.*, fig. S) is peculiar in being divided into two parts, a superior and an inferior. The superior part is the larger and arises from the dorsal third of the supraspinous fossa (*supras.*, pl. 38). The inferior part arises from a narrow line on the dorsal surface of the base of the proximal two-thirds of the spine of the scapula. The two parts join in a common tendon which is inserted on the greater tuberosity of the humerus. This is a strong muscle in the gopher; its action is to extend the humerus.

17. *Infraspinatus* (*infras.*, fig. S), arises from the proximal third of the infraspinous fossa and from the base of the proximal two-thirds of the spine of the scapula. It is inserted on the greater tuberosity of the humerus just caudal to the insertion of 16 (*infras.*, pl. 38). The infraspinatus flexes the humerus with relation to the scapula.

18. *Teres major* (*ter. ma.*, fig. T) arises from an impression on the proximal one-fourth of the axillary border of the scapula (*ter. ma.*, pls. 38, 39). The fibers pass ventrad and mesiad and join the latissimus dorsi in their lower third. The combined tendon passes to the mesial side of the humerus and is inserted just below the lesser tuberosity. The teres major is one of the flexors of the leg.

19. *Teres minor* (*ter. mi.*, fig. S) is closely related to the infraspinatus. It arises along the axillary border of the scapula on the lateral surface, and is inserted on the greater tuberosity of the humerus behind the insertion of the infraspinatus (*ter. mi.*, pl. 38). It is an unimportant flexor of the leg.

20. *Subscapularis* (*subsc.*, fig. T) covers the whole of the mesial surface of the scapula, arising from the proximal fourth of this surface and from a line along the axillary border (*subsc.*,

pl. 39). The tendon passes down under the coracoid process of the scapula, and is inserted on the lesser tuberosity of the humerus. The subscapularis is a flexor and adductor of the leg.

21. *Triceps brachii* (*tri.*, fig. S). This muscle is relatively more important in the quadrupeds than in man, since it must support a considerable part of the weight of the body in standing. And it is especially well developed in fossorial forms, in which it furnishes nearly all of the power for extending the forearm, a very important movement in digging. All three heads of the triceps are strongly developed in the gopher.

a. *Caput longum* arises from the distal three-fourths of the lateral surface of the axillary border of the scapula (*tri. long.*, pl. 38). This is the bulkiest of the three parts, and its insertion is nearest the end of the olecranon process.

b. *Caput laterale* arises from the posterior and lateral surfaces of the humerus in a line extending from a point just below the head down to the deltoid tuberosity (*tri. lat.*, pl. 38). It is intermediate in volume, and its insertion is on the lateral surface of the olecranon process and on the fascia over the origins of the extensor muscles of the hand (*tri. lat.*, fig. Q).

c. *Caput mediale* (*tri. med.*, fig. T) arises from the posterior and mesial surfaces of the humerus from a point just below the lesser tuberosity nearly to the distal extremity of the bone. Its insertion covers most of the cephalic surface of the olecranon process.

22. *Extensor antibrachii parvus* or *epitrochlearis* (*ex. ant. par.*, fig. T) is a slender, flat band of muscle fibers arising from the fascia of the teres major and latissimus dorsi, and inserted on the tip of the mesial border of the olecranon. It is a weak extensor of the forearm.

23. *Anconeus medialis* (*anc. med.*, fig. T) arises from the posterior surface of the internal supracondylar ridge of the humerus, to be inserted on the mesial surface of the olecranon process (*anc. med.*, pl. 39).

24. *Anconeus lateralis* (*anc. lat.*, fig. S) arises from the posterior surface of the external supracondylar ridge of the humerus, and is inserted on the lateral surface of the olecranon near its tip. The *anconeii* are weak extensors of the forearm; the *anconeus lateralis* is the smaller of the two and is not found in the rabbit.

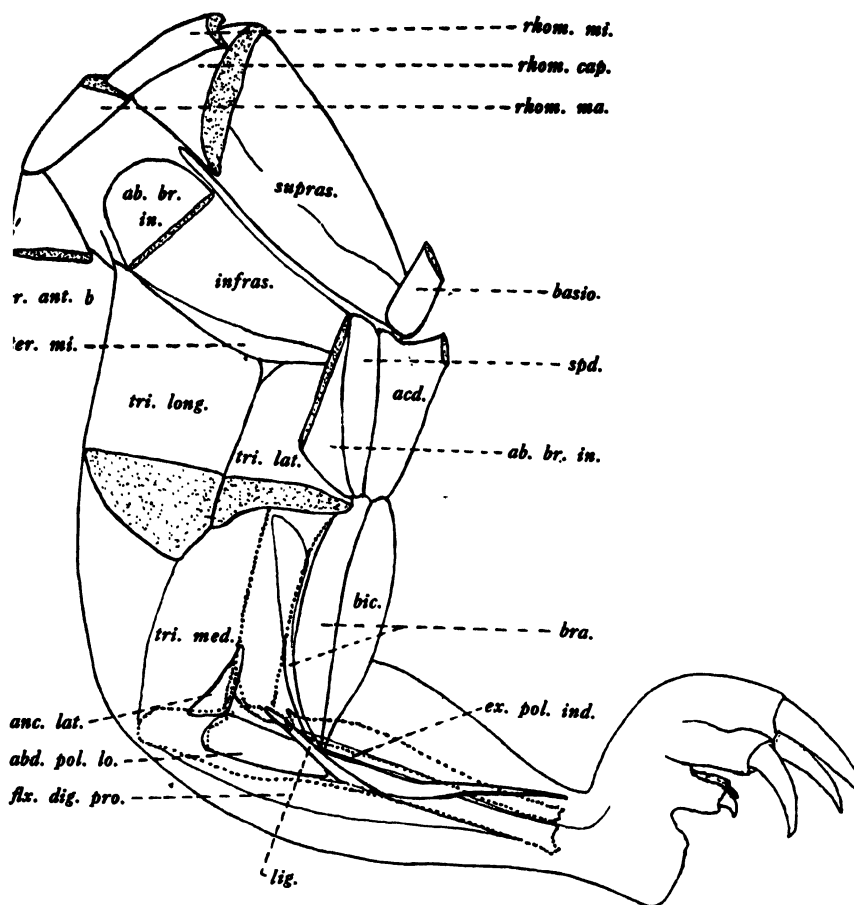


Fig. S. Lateral view of deep muscles of right thoracic limb of the gopher, $\times 2$.

ab. br. in.—abductor brachii inferior
abd. pol. lo.—abductor pollicis longus
acd.—acromiodeltoideus
anc. lat.—anconeus lateralis
basio.—basioclavicularis
bic.—biceps brachii
bra.—brachialis
ex. pol. ind.—extensor pollicis et indicis
fls. dig. pro.—flexor digitorum profundus
infras.—infraspinatus

lig.—external collateral ligament
rhom. cap.—rhomboideus capitalis
rhom. ma.—rhomboideus major
rhom. mi.—rhomboideus minor
ser. ant. b.—serratus anterior, thoracic portion
spd.—spinodeltoideus
supras.—supraspinatus
ter. mi.—teres minor
tri. long.—triceps, caput longum
tri. lat.—triceps, caput laterale
tri. med.—triceps, caput mediale

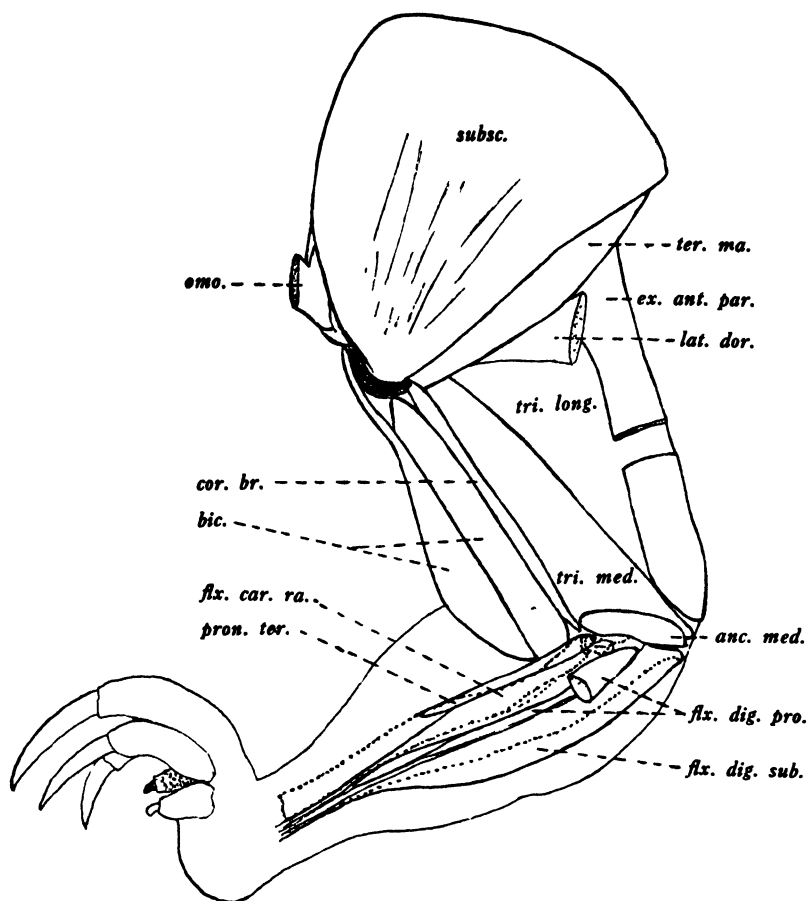


Fig. T. Mesial view of deep muscles of right thoracic limb of the gopher, $\times 2$.

anc. med.—anconeus medialis

cor. br.—coracobrachialis

ex. ant. par.—extensor antibrachii
parvus

flx. car. ra.—flexor carpi radialis

flx. dig. sub.—flexor digitorum sub-
limis

lat. dor.—latissimus dorsi

omo.—omohyoideus

pron. ter.—pronator teres

subsc.—subscapularis

ter. ma.—teres major

For other abbreviations see explanation of Fig. S.

25. *Biceps brachii* (*bic.*, figs. O, S, T) in the gopher has two heads; in this respect it differs from this muscle in the rabbits, ground squirrel and tree squirrel, in which the biceps has only the long or glenoid head. In the gopher and in the rat, however, the biceps also has the coracoid head, as in the human biceps.

a. *Caput longum* (*bic.*, fig. T) in the gopher arises from the upper margin of the glenoid cavity, and its tendon traverses the capsule of the shoulder joint.

b. *Caput breve* arises from the tip of the coracoid process of the scapula in common with the origin of the coracobrachialis. The two heads are separate nearly to their insertion, where they unite to form a common tendon which is attached to the ventromesial surface of the ulna and slightly to the radius, in common with the tendon of the brachialis (*bic.*, pl. 38, 39). The biceps is the principal flexor of the forearm.

26. *Coracobrachialis* (*cor. br.*, fig. T) arises from the coracoid process of the scapula and is inserted in a line along the mesial surface of the humerus for its distal two-thirds (*cor. br.*, pl. 39). This muscle is small and is an unimportant adductor of the arm.

27. *Brachialis* (*bra.*, fig. S) consists of a large lateral portion and a small mesial portion, the origins of which lie on either side of the deltoid tuberosity. The lateral origin occupies the posterior and lateral surfaces of the humerus for the proximal third of the bone. The mesial part arises from the base of the deltoid tuberosity (*bra.*, pl. 38, 39). The two parts join near the middle of the humerus, and are inserted on the ulna and radius in common with the biceps. This muscle, especially the lateral part, is a strong flexor of the forearm.

28. *Extensor carpi radialis longus* (*ex. car. ra. lo.*, figs. Q, R) arises on the cephalic surface of the external supracondylar ridge of the humerus, and is inserted on the dorsal surface of the base of the second metacarpal (*ex. car. ra. lo.*, pl. 38).

29. *Extensor carpi radialis brevis* (*ex. car. ra. br.*, figs. Q, R) arises on the cephalic surface of the external supracondylar ridge of the humerus just distal to the origin of 28, and is inserted on the dorsal surface of the base of the third metacarpal (*ex. car. ra. br.*, pl. 38). This is a stronger muscle than the preceding; the action of both muscles is to extend the manus and to render the carpal articulation rigid.

30. *Abductor pollicis longus* (*abd. pol. lo.*, fig. S) arises from the lateral surface of the ulna in a curved line from the ulno-humeral articulation to the middle of the bone (*abd. pol. lo.*, pl. 38). This muscle occupies the deeply grooved lateral surface of the ulna, passing beneath the greatly enlarged external collateral ligament, and becomes superficial only in the distal third of the fore-

arm. Here its tendon passes over the tendons of muscles 28 and 29 and is inserted on the radial side of the base of metacarpal 1. This muscle is an extensor of the manus and pollex, and possibly also has a supinating action. It doubtless corresponds to the extensor ossi metacarpi pollicis in man.

31. *Extensor digitorum communis* (*ex. dig. com.*, fig. Q) arises by the common extensor tendon from the external condyle of the humerus. Near its origin it begins to divide and its parts end in four tendons which pass deeply under the annular ligament of the wrist. The tendons then diverge and are inserted into the bases of the terminal phalanges of digits 2, 3, 4, and 5 (*ex. dig. com.*, pl. 38). This muscle extends first the digits and then the entire manus.

32. *Extensor pollicis et indicis* (*ex. pol. ind.*, fig. S) arises in common with the extensor group of muscles, on the lateral condyle of the humerus. Its tendon accompanies those of the preceding muscles under the annular ligament. It becomes superficial in the metacarpal region, and divides into two parts, the mesial of which is inserted at the base of the distal phalanx of the pollex, and the lateral on the distal end of the dorsal surface of metacarpal 2. Its action is to extend digits 1 and 2, and by further action, the manus.

33. *Extensor digiti quinti proprius* (*ex. dig. q. pr.*, fig. Q) arises by the common extensor tendon, and is inserted by two tendons, one in the distal end of the dorsal surface of metacarpal 5, and the other in the base of the terminal phalanx of digit 5 (*ex. dig. q. pr.*, pl. 38). This muscle extends the fifth digit and, like the preceding, serves to stiffen the carpal articulation.

34. *Extensor carpi ulnaris* (*ex. car. ul.*, fig. Q) arises on the lateral surface of the ulna in a curved line just posterior to the origin of the abductor pollicis (*ex. car. ul.*, pl. 38), and is inserted on the base of the lateral surface of metacarpal 5. This muscle extends and abducts the wrist.

35. *Palmaris longus* (*palm. lo.*, fig. R) arises on the internal condyle of the humerus in common with the flexor group of muscles. It is superficial for its entire length, and is inserted into the palmar fascia. In the gopher this muscle is relatively large and is a strong flexor of the manus.

36. *Flexor carpi ulnaris* (*flx. car. ul.*, fig. R).—This is the largest muscle in the forearm of the gopher; it is superficial on the whole caudal surface of the forearm. This muscle arises on the

mesio-caudal surface of the olecranon process of the ulna (*flx. car. ul.*, pl. 39), and is inserted into the tip of the pisiform bone. The length of the latter gives the muscle a strong leverage and makes it a very powerful flexor of the manus.

37. *Flexor digitorum sublimis* (*flx. dig. sub.*, fig. T) arises from the common flexor tendon and the adjacent part of the mesial surface of the ulna, and passes distad beneath the palmaris. In the distal third of the forearm it ends in four tendons which pass beneath the bony arch formed by the falciform and pisiform bones, and are inserted into the bases of the second phalanges of digits 2, 3, 4, and 5 (*flx. dig. sub.*, pl. 39). This muscle flexes first the digits, and, by continued action, the manus.

38. *Flexor digitorum profundus* (*flx. dig. pro.*, fig. S) arises by three heads. The largest head takes origin on the caudal and mesial surfaces of the ulna from the base of the olecranon to the middle of the bone (*flx. dig. pro.*, pl. 39); this head is superficial on the lateral side of the forearm. The second head arises by the common flexor tendon from the mesial condyle of the humerus. This part of the muscle is superficial on the mesial side of the forearm (*flx. dig. pro.*, fig. T). The third and smallest portion arises from a narrow line along the proximal third of the ventro-mesial border of the ulna. These three parts unite to form a common tendon which passes through the annular ligament beneath the tendons of the preceding muscle. The tendon then divides into five parts which are inserted into the palmar surfaces of the bases of the terminal phalanges of all five digits. This muscle is a stronger flexor of the digits and manus than the *flexor digitorum sublimis*.

39. *Flexor carpi radialis* (*flx. car. ra.*, fig. T) arises from the common flexor tendon and is inserted on the palmar surface of the base of metacarpal 2. This is a deep muscle in the upper two-thirds of the forearm. It is a flexor of the carpus.

40. *Pronator teres* (*pron. ter.*, figs. R, T) arises from the internal condyle of the humerus and is inserted on the antero-mesial surface of the radius near its middle (*pron. ter.*, pl. 39). It is probable that this muscle has little pronating action, but serves rather as a flexor of the forearm.

41. *Supinator* arises from the external condyle of the humerus and is inserted on the proximal third of the cephalic surface of the radius (*sup.*, pl. 38). This muscle is probably homologous with the muscle known as the brachioradialis in the cat, but it more

nearly corresponds to the human supinator. Its action doubtless gives the slight supination of the manus which has been noted in the gopher (Merriam, 1895, p. 17; Stephens, 1906, p. 142).

42. *Pronator quadratus* (*pron. quad.*, pl. 39) is a thin layer of fibers arising on the mesial surface of the distal third of the ulna, and inserted on the mesial surface of the distal third of the radius. It furnishes the chief pronating force in the gopher and antagonizes the action of the supinator.

GROUPING OF MUSCLES ACCORDING TO FUNCTION

In considering the functions of muscles it is convenient to study together those which have a similar action. We have, therefore, divided the muscles of the thoracic limb of the gopher and of the other rodent forms into eight functional groups, and in the following volumetric work the volumes of all the muscles of the group are used in comparisons, rather than the volumes of the individual muscles.

The principal movements which the scapula is capable of performing may be divided into two classes: (1) Rotary movements around a center located in the flat part of the bone and perpendicular to its surface; (2) Gliding movements of the bone as a whole over the thoracic wall. The muscles attached to the clavicle may be considered as assisting in one or another of these movements. We shall not attempt a further analysis of these movements, or the separation of the shoulder muscles into sub-groups; the following considerations make it inadvisable to do this: (1) These movements are very complex and the same muscle often participates in both of the above classes of movements; (2) The variations in origins and insertions found in the different forms make homologous muscles uncomparable in their action. All of the muscles which move the shoulder girdle are therefore grouped together, as follows, the numerals referring to the numbers of the muscles in the descriptive list (pp. 463 to 481):

Group 1. Muscles which move the shoulder girdle:

- 2 Trapezius
- 3 Rhomboideus capitalis
- 4 Rhomboideus minor
- 5 Rhomboideus major
- 7 Sternomastoideus
- 8 Cleidomastoideus
- 9 Bascioclavicularis

- 10 Omohyoideus
- 11c Pectoralis tertius
- 12 Subclavius
- 13 Serratus anterior

The remainder of the muscles of the anterior limb may be divided into two main classes: (A) muscles from the body to the humerus (group 2), and (B) muscles of the arm proper (groups 3 to 8, inclusive). In considering the latter class, the muscles of the arm, it is convenient to think of the arm as consisting of three parts, the upper arm, the forearm, and the hand. Each of these parts has a system of extensor muscles, or those which tend to straighten it with relation to the bone situated next proximad, and a system of flexor muscles, or those which tend to flex the given part in relation to the bone next above it. It is of course obvious that the extensors and flexors of a given part are located in the part next proximad; thus the flexors and extensors of the upper arm are grouped around the scapula, the flexors and extensors of the forearm around the humerus, and the flexors and extensors of the hand around the radius and ulna. Six groups of muscles of the limb proper will therefore be considered.

The only muscles which do not fall into any of the above eight groups are the supinator and the pronator quadratus. These two muscles have not been taken into account in the volumetric work.

In the groups given below the individual muscles are listed in the order of their size in the gopher, the largest being placed first.

Group 2. Muscles from the body to the humerus; these muscles pull the arm downward and backward:

- 6 Latissimus dorsi
- 11b Pectoralis secundus
- 11d Pectoralis quartus
- 11a Pectoralis primus
- 1 Cutaneus maximus

Group 3. Extensors of the upper arm:

- 16 Supraspinatus
- 14a Acromiodeltoideus
- 14b Spinodeltoideus
- 26 Coracobrachialis

Group 4. Flexors of the upper arm:

- 20 Subscapularis
- 17 Infraspinatus
- 15 Abductor brachii inferior
- 18 Teres major
- 19 Teres minor

Group 5. Extensors of the forearm:

- 21 Triceps brachii
- 22 Extensor antibrachii parvus
- 23 Anconeus medialis
- 24 Anconeus lateralis

Group 6. Flexors of the forearm:

- 25 Biceps brachii
- 27 Brachialis
- 40 Pronator teres

Group 7. Extensors of the hand:

- 29 Extensor carpi radialis brevis
- 31 Extensor digitorum communis
- 28 Extensor carpi radialis longus
- 34 Extensor carpi ulnaris
- 33 Extensor digiti quinti proprius
- 30 Abductor pollicis longus
- 32 Extensor pollicis et indicis

Group 8. Flexors of the hand:

- 36 Flexor carpi ulnaris
- 38 Flexor digitorum profundus
- 37 Flexor digitorum sublimis
- 35 Palmaris longus
- 39 Flexor carpi radialis

VOLUMETRIC MEASUREMENTS

As a basis for functional comparison of similar muscles in different forms we must have an idea of the force normally exerted by such muscles. It has been shown by physiological experiment that the volume of a muscle is a true indicator of the work it can perform. Foster (1896, p. 124) expresses this law as follows:

If two muscles are unequal both in length and sectional area, the work done will be the greater in the one which has the greater bulk, which contains the greater number of cubic units. In speaking, therefore, of the work which can be done by a muscle, we may use as a standard a cubic unit of bulk, or, the specific gravity of the muscle being the same, the unit of weight.

Volume was selected rather than weight as an indicator of strength, because it seemed to be better adapted for testing both the bones and the muscles.

The volumes of the various structures were determined by immersing them in graduated glass vessels of appropriate sizes containing water, and noting the displacement. The chief objection to this method is that the amount of liquid contained in the tissues

influences their volume. This error was reduced to a minimum, however, by keeping the specimens well moistened with water during dissection, and by being careful that before immersing the structures they were neither too dry nor contained an excess of water. The fact that the preservative used (80 per cent alcohol) abstracts water from tissues and reduces their volume is of no importance since only relative volumes are required, and all measurements were taken in exactly the same manner. If weight had been used as a criterion of strength, the amount of water in the tissues would have caused as great an error as in the volumetric method.

The mammals used were usually skinned in the fresh state, but sometimes they were placed in the preservative before being skinned, the abdomen and thoracic cavity being always well injected with alcohol. In either case, when the animal was skinned care was taken to dissect out and save as much of the cutaneus maximus muscle as possible. After the specimen had been left in the preservative for several days to harden, dissection was begun by carefully separating and detaching at their origins and insertions the muscles which bind the anterior limb to the body. As each muscle was removed its volume was measured, as described above. When all the muscles which hold the leg to the body had been removed, the sternoclavicular articulation was separated, and the volume of the detached leg was measured. To this figure the sum of the volumes of the shoulder muscles already removed was added, and the total volume was considered as 100 per cent. The muscles of the leg proper were then dissected out and measured separately in the same way. After all the muscles had been removed the volume of the leg skeleton, including the scapula and clavicle, and the hand, was measured. The volumes of the muscles composing each different group were now added, and the bulk of the whole functional group obtained. Finally, the percentages of the volumes of each group to the total volume of the leg was determined. The results of these computations are given in table 1, p. 485. No actual volumes are given in the table, all volumes being reduced to percentages of the total bulk of the leg and shoulder, in order to make them comparable.

It will be noted that the total volume accounted for is less than 100 per cent. This is due to the fact that in dissection it was necessary to remove various structures, such as fat, fascia, blood

vessels, nerves, and lymphatics, the volume of which was not determined.

The figures given are from average measurements of several individuals in all cases except the Belgian hare; only one of these animals was dissected.

TABLE 1

TABLE SHOWING RELATIVE VOLUMES OF MUSCLE GROUPS IN THE SEVEN FORMS DISSECTED. IN PERCENTAGES, CONSIDERING THE WHOLE VOLUME OF THE ARM PLUS VOLUME OF THE BONES AND MUSCLES OF THE SHOULDER, AS 100 PER CENT.

Muscle Groups	Pocket gopher	Ground squirrel	Brown rat	Jack rabbit	Cottontail	Belgian hare	Red squirrel
Group 1, shoulder-girdle muscles.....	20.6	22.9	16.0	17.4	19.1	21.4	14.8
Group 2, draw humerus downward and backward	15.3	18.5	37.3	18.4	12.9	13.0	23.6
Group 3, extensors of upper arm.....	5.7	6.7	5.4	7.2	12.1	7.9	5.3
Group 4, flexors of upper arm.....	9.6	9.6	6.8	13.6	11.5	14.8	9.8
Group 5, extensors of forearm.....	7.9	10.5	9.2	11.7	10.7	10.1	11.9
Group 6, flexors of forearm.....	4.0	3.5	2.1	2.3	2.6	3.5	5.5
Group 7, extensors of hand.....	3.5	4.2	2.0	1.4	1.6	2.2	4.3
Group 8, flexors of hand.....	6.1	4.9	3.0	2.9	2.9	3.5	5.3
Bones and hand, after removal of arm muscles	17.5	10.7	9.7	18.2	11.3	16.3	14.4
Total volume accounted for.....	90.2	91.5	91.5	93.1	84.7	92.7	94.9

DEDUCTIONS FROM VOLUMETRIC FIGURES

It now remains to be seen whether or not the data accumulated indicate any correlation between the habits of the different rodents and the development of the various muscle groups. The relation of habit to volume and shape of bones in the different types has already been discussed (see p. 451). The muscles of group 1 are relatively unimportant in the specialized movements of each mammal. As has been noted, the actions of these muscles are very complex, and a simple correlation with habits of life could not be expected. While the volume of these muscles varies from 16 per cent in the rat to 22.9 per cent in the ground squirrel, no explanation of this variation is apparent.

Group 2 is composed of muscles which draw the humerus downward, backward and inward. This movement would seem to be about equally useful in climbing trees, in digging, and in running;

probably the climbing habit would call for a greater use of these muscles. An examination of table 1 shows this functional group to be enormously larger in the rat than in any of the other forms. This is explained, however, by the very great development of the cutaneous maximus muscle, which in the rats dissected composed from 14.4 per cent to 20 per cent of the whole volume of the leg and shoulder. Since much of this muscle has no effect on the movement of the leg, it is evident that group 2 is not larger than would be expected in the rat. The chickaree, our climbing type, shows the next largest muscles of group 2, and in this form the cutaneous maximus is very small. The jack rabbit and the two digging rodents rank close together in size of this group. Contrary to what might be expected, it is relatively smaller in the gopher than in the ground squirrel. But this is accounted for when we consider the point of insertion of the principal muscles of this group. In the gopher the insertion is much farther distad on the humerus than in the ground squirrel, thereby giving a greater mechanical advantage to these muscles in the former rodent than in the latter. This is an example of smaller volume in muscles being compensated for by advantageous insertion. The Belgian hare and the cottontail have group 2 least developed.

Group 3, the extensors of the upper arm, are best developed in the three rabbits, especially in the cottontail. No explanation of this is apparent, unless it is associated with the fact that the scapulo-humeral articulation is more movable in the rabbits, as indicated by the larger surface of the head of the humerus. In the other forms this group is very nearly of the same relative size.

Group 4, the flexors of the upper arm, are also largest in the rabbits. Development of this group also would be associated with a more movable humerus such as we should expect to find in types specialized for running. The fact that this group is best developed in the Belgian hare is not explained by the above reasoning, however. Here, as in group 3, the other rodents examined show little difference in the development of these muscles.

Group 5, the extensors of the forearm, is one which we should expect to find best developed in the fossorial rodents, since these muscles are undoubtedly much used in the act of digging. But table 1 shows this not to be the case; in fact, group 5 is smaller in the gopher than in any of the other forms. The explanation of this seeming lack of correlation is, however, apparent when we

examine the insertion of the triceps, the muscle which makes up over nine-tenths of the volume of the group. The triceps is inserted on the olecranon, and this process in the gopher is much longer than in the other forms. Table 2 shows the length of the olecranon compared to the whole length of the ulna in the seven forms. In the gopher the olecranon composes 25 per cent of the length of the bone; the ground squirrel ranks second in relative length of this process, and the rat third. The three fossorial forms thus have the largest olecranon process.

Since, as we have seen, the strength of a muscle is directly proportional to its volume, we may for a moment let the figures representing the relative volume of group 5 in the various forms (see table 1) stand for the actual pull which it applies to the olecranon. Thus in the gopher the extensors of the forearm would pull with a force equal to 7.9 units, in the ground squirrel 10.5 units, in the rat 9.2 units, etc. Now if there were no mechanical differences in the structure of the limb, these muscles would be considerably less efficient in the gopher than in any of the other forms. But the ulna acts as a lever of the first class with the articulation as its fulcrum, the olecranon as its power arm, and the portion of the bone distal to the articulation as the work arm. The following physical law governs the action of levers: The product of the power by the length of the power arm is equal to the product of the work by the length of the work arm. We may properly use the relative size of the muscles of group 5 to represent the power, and we may easily measure the power arm and the work arm of this lever; hence we may apply the law of levers and compute the actual work delivered at the end of the forearm. This has been done for each of the seven forms, as shows in table 2.

TABLE 2

TABLE SHOWING UNITS OF WORK PERFORMED BY MUSCLES OF GROUP 5 IN THE DIFFERENT FORMS, COMPUTED ACCORDING TO THE LAW OF LEVERS

	Per cent of power arm (olecranon) to whole of ulna	Power arm	× Power	= Work arm	× Work
Pocket gopher	25.8	.718 cm.	7.9	2.064 cm.	2.74
Ground squirrel	18.3	.732	10.5	3.262	2.35
Brown rat	17.2	.56	9.2	2.63	1.92
Jack rabbit	10.6	1.21	11.7	10.121	1.39
Cottontail	12.3	1.07	10.7	7.605	1.50
Belgian hare	15.4	1.21	10.1	6.64	1.84
Chickaree	15.2	.548	11.9	3.048	2.13

It is evident from the above table that the force of the movement produced by muscles of group 5 is considerably greater in the gopher than in any of the other forms, notwithstanding its smaller relative size. The ground squirrel ranks second in the available work developed by these muscles. Of course, what is gained in force is lost in speed of movement, but speed is not so essential in the digging forms as is strength. In the jack rabbit, however, rapidity of movement is essential, and we find that in this animal force is sacrificed for speed. The three rabbits stand lowest as regards the real force of these muscles, but highest in the speed of movement produced. It is not apparent why group 5 in the chickaree should be so strong as it appears in table 2.

While complete accuracy is not claimed for the figures in table 2, they serve to bring out the fact that the efficiency of a muscle or group of muscles is to a great extent dependent upon its point of insertion.

What has been worked out in detail in this particular case is only an example of what could undoubtedly be found in every part of the mechanical structure of these forms. In the fossorial type we should find speed sacrificed for force, and in the cursorial forms force sacrificed for speed.

Group 6, the flexors of the forearm, as shown by table 1, are relatively larger in the chickaree than in any of the other rodents. This is what would be expected, since these muscles are of great importance in climbing trees. Of the other rodents this group is smallest in the rabbits.

Group 7, the extensors of the hand, are largest in the two squirrels and smallest in the rabbits. This is another case in which the correlation between habit and anatomy is not clear. In all these cases there are undoubtedly some influencing factors which we have not taken into account.

Group 8, the flexors of the hand, we should expect to find largest in the digging and climbing forms, and this is what table 1 actually indicates. The group is relatively largest in the gopher, and in this animal its force is increased by the fact that the largest muscle in the group, the flexor carpi ulnaris, is inserted on the high pisiform bone. The chickaree ranks next in development of this group, and the ground squirrel third. In the rabbits these muscles are small.

SUMMARY

In the course of this study of structural specialization among rodents, certain facts have become apparent which seem applicable outside the limits of the relatively narrow field covered. We therefore venture to suggest the following conclusions as generally true in other forms, as well as among rodents:

(1) In proportion to their size, fossorial forms have a stronger mechanical equipment than forms adapted to either the cursorial or the arboreal mode of life. The ground being the densest medium in which animals live, those forms which live in it must be provided with the heaviest and strongest mechanism of motion. And we find this mechanism developed in a definite direction, to the end that a particular set of movements may be easily and powerfully performed.

(2) The bony levers found in the animal body are accurately adjusted to the strength of the muscles which operate them, and to the kind of movement which is most needed. The gopher needs to make short, powerful strokes, while the rabbit requires long, swift movements. The bony levers are so arranged that in the former type force is gained at the cost of speed, while the latter speed is gained by sacrificing force.

(3) The idea that irregularity of outline of bones indicates strength of the osseo-muscular machine is correct. We find the most irregular bones associated with power in the digging types, especially in the gopher. On the other hand, smooth bones are associated with swiftness of movement in the cursorial types.

(4) Volume of bones is not a criterion of strength of body. The relative volume of the bones in the jack rabbit is larger than in any of the other forms examined.

(5) The particular sets of muscles which are most used are either actually largest, for example, the flexors of the forearm of the chickaree, or they are made functionally strongest by the arrangement of the bony levers, as in the extensors of the forearm in the gopher. Hence the force of a given set of muscles depends both on its size and on its point of attachment to the mechanical system.

(6) Domestication reduces specialization. The typical cursorial modifications have either disappeared or have been much reduced in the Belgian hare.

Transmitted May 1, 1914.

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PLATE 38

Lateral view of skeleton of left thoracic limb of the gopher, showing origins (in blue) and insertions (in red) of muscles, $\times 2\frac{3}{4}$.

- | | |
|--|--|
| <i>ab. br. in.</i> —abductor brachii inferior | <i>ex. pol. ind.</i> —extensor pollicis et indicis |
| <i>abd. pol. lo.</i> —abductor pollicis longus | <i>infras.</i> —infraspinatus |
| <i>acd.</i> —acromiodeltoideus | <i>omo.</i> —omohyoideus |
| <i>anc. lat.</i> —anconeus lateralis | <i>rom. cap.</i> —rhomboideus capitalis |
| <i>bic.</i> —biceps brachii | <i>rom. ma.</i> —rhomboideus major |
| <i>bra.</i> —brachialis | <i>rom. mi.</i> —rhomboideus minor |
| <i>ex. car. ra. br.</i> —extensor carpi radi-
alis brevis | <i>spd.</i> —spinodeltoideus |
| <i>ex. car. ra. lo.</i> —extensor carpi radi-
alis longus | <i>sup.</i> —supinator |
| <i>ex. car. ul.</i> —extensor carpi ulnaris | <i>supras.</i> —supraspinatus |
| <i>ex. dig. com.</i> —extensor digitorum
communis | <i>ter. ma.</i> —teres major |
| <i>ex. dig. q. pr.</i> —extensor digiti quinti
proprius | <i>ter. mi.</i> —teres minor |
| | <i>trap.</i> —trapezius |
| | <i>tri. long.</i> —triceps, caput longum |
| | <i>tri. lat.</i> —triceps, caput laterale |
| | <i>tri. med.</i> —triceps, caput mediale |

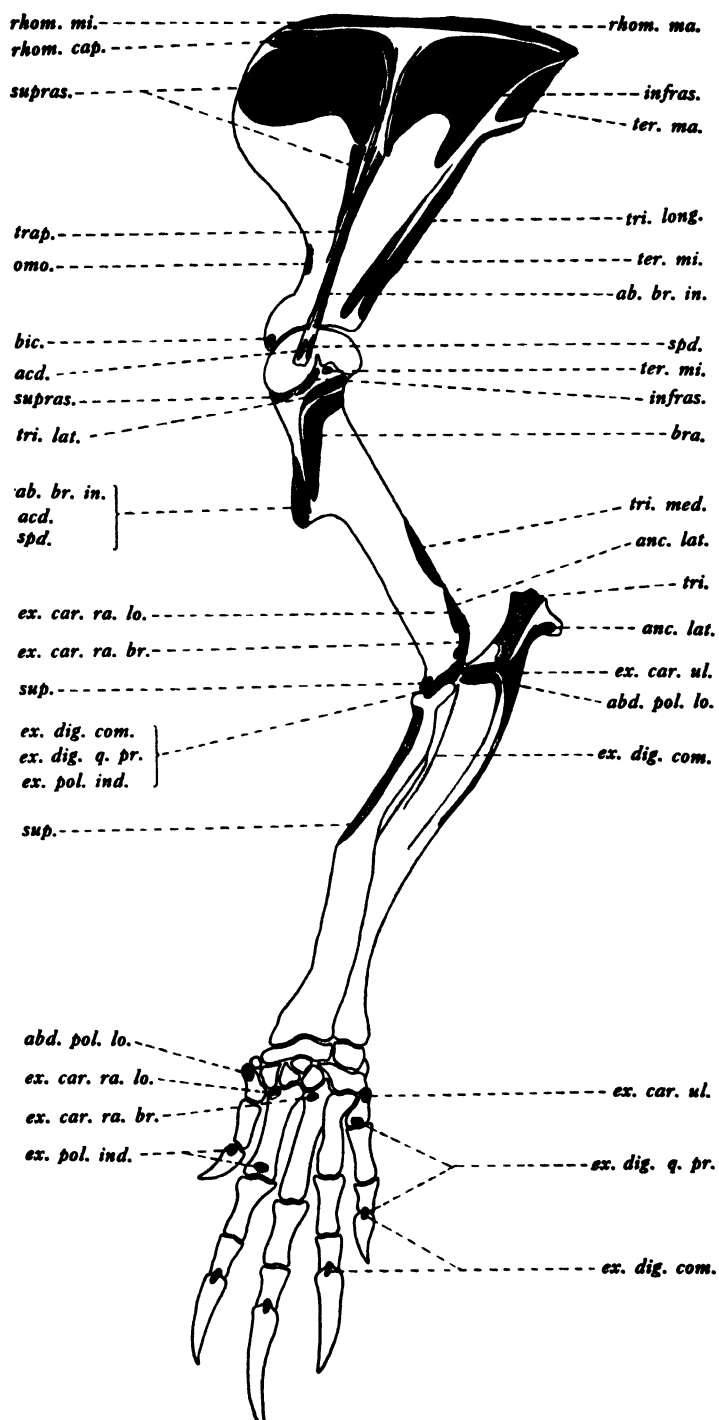


PLATE 39

Mesial view of skeleton of left thoracic limb of the gopher, showing origins (in blue) and insertions (in red) of muscles, $\times 2\frac{1}{2}$.

anc. med.—anconeus medialis

bic.—biceps brachii

bra.—brachialis

cor. br.—coracobrachialis

cut. max.—cutaneus maximus

ex. ant. par.—extensor antibrachii
parvus

flx. car. ra.—flexor carpi radialis

flx. car. ul.—flexor carpi ulnaris

flx. dig. pro.—flexor digitorum pro-
fundus

flx. dig. sub.—flexor digitorum sub-
limis

lat. dor.—latissimus dorsi

palm. lo.—palmaris longus

pec. pri.—pectoralis primus

pec. quar.—pectoralis quartus

pec. sec.—pectoralis secundus

pec. ter.—pectoralis tertius

pron. quad.—pronator quadratus

pron. ter.—pronator teres

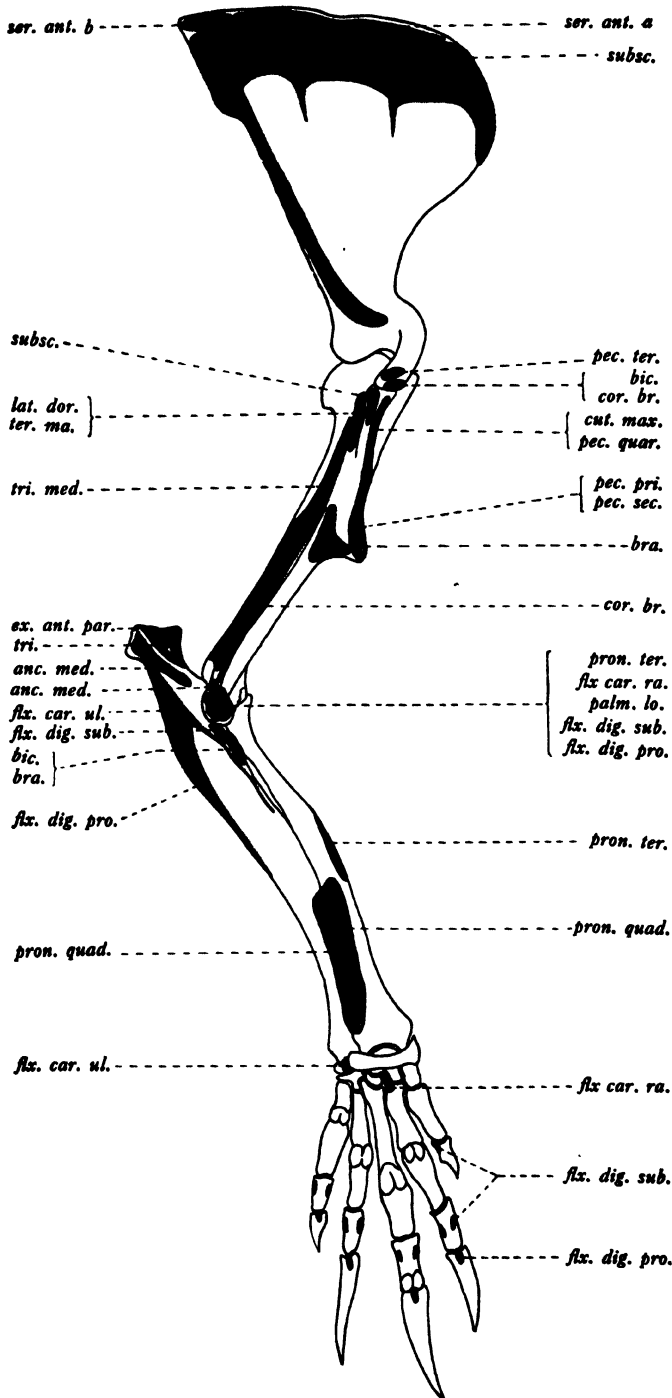
ser. ant. a.—serratus anterior, cervical
portion

ser. ant. b.—serratus anterior, thoracic
portion

subsc.—subscapularis

ter. ma.—teres major

tri. med.—triceps, caput mediale



THE INHERITANCE OF EXTRA BRISTLES IN *DROSOPHILA MELANOGASTER* MEIG.

BY

EDNA M. REEVES

The object of this paper is to show the inheritance of extra bristles in *Drosophila melanogaster* Meig. (= *D. ampelophila* Leow), and to see if selection had any influence on the results. Similar work on this subject has been done by Edwin Carleton MacDowell (1915). The results obtained in my work agree in part and disagree in part with his conclusions.

So many experiments have been made of late with this little fly, *Drosophila*, by Morgan and his students, that it is familiar to all zoological workers. The character used in this case was the number of bristles, its inheritance and variation. The bristles, normally four in number, appear on the dorsal surface of the thorax and form a regular rectangular pattern, thus: : : The flies used originally came from Professor Morgan's stock in New York, but have been bred in the laboratory of genetics at Berkeley for two years.

In a mass culture of 235 flies, five, or 2.97 per cent, were found with one extra bristle. Three of these were females and two were males. All of these were mated with normals and an account kept of the subsequent generations. After the first mating, three kinds of crosses were made: (1) normal \times normal, (2) normal \times extra, (3) extra \times extra.

The bottles and food were sterilized to prevent any infection. The bottles were labelled and the hatchings were immediately removed from the bottles to prevent any overlapping of generations. The

virginity of the females was assured by using only those whereof the time of hatching was known and removing them from the bottles immediately, before the wings had uncurled or the pigment had formed to any extent.

Besides the extra-bristled flies, other variations were found, incidentally, one club-winged mutant, one individual with only one wing and with head and thorax bent much to one side. There were also seven beaded-winged mutants, but as they were exceedingly non-viable and sterile no offspring were obtained.

Abdominal variations in banding were found and were carried through three generations with a verification of Morgan's theory that the inheritance is dependent on a factor of environment, namely moist food. After the character makes its appearance it may be kept or masked by the character of the food. It is not induced to appear by moist food, but its presence and inheritance is made manifest by the continuance of moist food.

An inherited difference in pigmentation was also observed. It occurred in the shape of a shield on the thorax between the bristles, finally increasing into a trident with the ends running forward to the head. There was also a marked irregular line of pigmentation extending transversely in a jagged line between the anterior bristles. Lack of time prevented extensive study of this variation.

All the flies were carefully examined throughout for other possible differences, but with the above-mentioned exceptions the individuals were uniform in all their characters. There were, therefore, no facts on which it might be possible to base an assumption that the various ratios obtained were explainable through linkage with other characters.

Five strains, X, Y, Z, A, and B, were used, and the bristles of 4500 flies were examined.

I wish to express my sincere gratitude to Professor R. Ruggles Gates, who criticized and made suggestions on the work from time to time.

CROSSING EXPERIMENTS

As has been said, the normal number of the bristles is four, forming a rectangular pattern on the dorsal surface of the thorax. The exact positions of the extra bristles are not inherited, but they occur in random positions on the thorax. However, more often than not, they are in line with the normal bristles. Following are some of the arrangements:

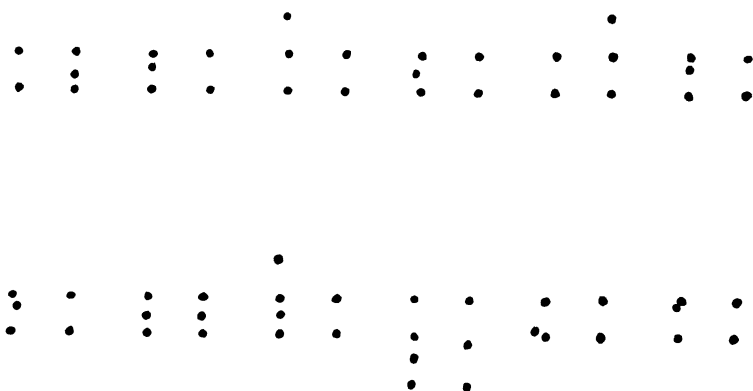


Fig. 1.—Showing arrangements of extra bristles on the thorax of *Drosophila melanogaster*.

From the original stock, when normals were mated with normals only normals were produced, but when those with five bristles were mated with normals the results were as shown in table I. In all matings in this paper, unless otherwise mentioned, brothers and sisters were crossed.

In table I each generation was bred in mass, obtained from the normals of the previous generation, the *extras* being removed and bred separately.

TABLE I
MASS CULTURES FROM NORMALS IN FOUR GENERATIONS

Family—	F ₁			F ₂			F ₃			F ₄			incomplete hatching		
	N.	ex.	Per cent	N.	ex.	Per cent	N.	ex.	Per cent	N.	ex.	Per cent	N.	ex.	Per cent
Y, ex. × N.	158	9	4.76	101	13	11.11	106	0	.0	105	1	.94	50	0	.0
X, ex. × N.	19	0	.00	127	2	1.05	85	2	2.4	100	0	.00	85	3	3.4
A, ex. × N.	90	1	1.09	75	1	1.32	90	0	.0	100	3	3.00	85	3	3.4

As might be expected, a fluctuating result was obtained when normals were extracted from the matings between two *extras*, in various families, and were then bred together in mass in subsequent generations. The results are shown in table II.

TABLE II
MASS CULTURES OF NORMALS EXTRACTED FROM MATINGS BETWEEN EXTRAS

Family—	F ₂			F ₃			F ₄			F ₅		
	N.	ex.	Per cent	N.	ex.	Per cent	N.	ex.	Per cent	N.	ex.	Per cent
X ₂	101	15	14.85	101	2	1.9	95	6	5.8
A ₂	38	5	12.15	105	1	.95	93	1	1.07	87	1	1.1
Y E	40	5	6.6	93	1	1.07	27	1	*3.5

* Incomplete hatching.

In the F_2 generation of X two *extras* were bred together. Subsequent generations from this cross were called X_5 . The same thing is true in the A family in the F_1 generation, and subsequent generations are called A_5 .

Tables III, IV, V, and VI show the results of crossing normals with *extras* in successive generations. Table VII shows the crosses between *extra* and *extra*.

The *extras* used for breeding in the tables below appeared in the crosses of normal with *extra* in Table I.

TABLE III

F_2 RESULTS OF MATINGS BETWEEN NORMAL AND EXTRA F_1 SIBS

Family—	Bottle letter	N.	ex.	N.	ex.	Per cent
Y	d	♀	♂	73	7	6.25
	i	♂	♀	48	9	15.
	j	♀	♂	102	2	1.96
	e	♂	♀	48	9	15.79
A_5	a	♀	♂	38	5	13.15

TABLE IV

F_2 RESULTS OF MATINGS BETWEEN NORMAL AND EXTRA F_2 SIBS

Family—	Bottle letter	N.	ex.	N.	ex.	Per cent
Y	A	♂	♀	7	0	00
	B	♂	♀	29	2	3.22
	C	♀	♂	9	0	00
	i	♀	♂	100	5	5.66
	e	♂	♀	100	3	33.3

TABLE V

F_4 RESULTS OF MATINGS BETWEEN NORMAL AND EXTRA F_3 SIBS

Family—	Bottle letter	N.	ex.	N.	ex.	Per cent
X_5	e	♂	♀	90	1	1.11
	d	♂	♀	100	6	5.66
	a	♂	♀	23	3	12.3
Y	E ²	♂	♀	100	3	33.3
	g ¹	♂	♀	95	1	1.68
A_5	c ¹	♂	♀	60	4	6.2

TABLE VI

F_5 RESULTS OF MATINGS BETWEEN NORMAL AND EXTRA F_4 SIBS

Family—	Bottle letter	N.	ex.	N.	ex.	Per cent
X	A ₁	♂	♀	60	3	4.7
	A ₂	♂	♀	50	1	1.9
A_5	ab	♂	♀	80	2	2.4
	C'b	♂	♀	70	3	4.1
X_5	d ₅	♀	♂	42	1	2.3

TABLE VII
EXTRA × EXTRA

Family—	Bottle letter	Number of extra bristles		N.	ex.	Per cent
F ₂ Y	e ²	♂ ²	♀ ³	48	6	11.11
	E	1	1	70	5	6.6
	F	1	1	88	7	4.21
	g	1	1	18	5	21.8
	d ⁴	1	1	10	4	28.5
	d ³	1	1	60	15	20.00
F ₂ X	a	1	2	76	10	11.6
	f	1	1	47	7	7.84
	xc	1	1	40	5	11.11
	x ₅	1	1	106	15	14.85
F ₂ X ₅	f ₂	1	1	50	14	28.
	c ²	1	1	23	6	20.3

These tables show that *extra* mated with *extra* gives a greater and a steadier percentage of extra-bristled than when normals were crossed with *extras*.

THE EFFECT OF ENVIRONMENT

1. *The Influence of Food.*—In seeking causes for the variability in the number of extra bristles, observations were made on certain environmental influences, food and temperature.

It seemed to make no difference in the number of extra bristles whether the food was moist or dry, as practically the same number of extra-bristled flies appeared under either set of conditions. Thus the variation differed from the abdominal variation described by Morgan (1915), in which moist food was the controlling factor.

As it is impossible to keep the bananas used for food at the same degree of acidity, and as *extras* appeared in all cultures, the degree of acidity can play no important part.

The abundance of food, also, could not play an important part, as the extra-bristled flies occurred most often in the middle of the counts and continued to appear up until the end. The normals occurring in inbred selected culture appeared all through the hatchings but in larger numbers at first, thus differing from MacDowell's (1915) result, who found that the extra-bristled flies appeared in larger numbers in the first part of the hatching.

Table VIII gives a few examples from the families studied. In each case a pair of flies was placed in a bottle and then, before their eggs began to hatch, they were removed to a second bottle, where a new batch of eggs was laid. These hatchings are shown in table VIII.

TABLE VIII

SHOWING DAILY HATCHINGS OF NORMALS AND EXTRAS

Mating Letter	Bottle	Month	Day	—Bristles—	
Y d ^a	1	March	6	4	5
			7	14	
			8	16	1
			9	12	
			10	6	6
			11	5	5
			12	7	3
	2		13	10	
			14	12	
			15	8	3
			16	9	4
			17	3	2
			18	3	1
X ₃ c	1	March	10	7	0
			11	4	1
			12	10	1
			13	12	3
			14	3	1
	2		15	4	
			16	4	
			17	16	
			18	13	2
			19	3	1
			20	4	1
			21	5	
X _a	1	March	13	6	3
			14	20	3
			15	28	4
			16	7	2
			17	5	1
			18	3	
	2		19	3	
			20	8	
			21	20	2
			22	7	3
			23	4	1
			24	2	1

If abundance of food were the prevailing factor, more extra-bristled flies should occur in the first and second day's hatchings, but, as this is not the case, it seems safe to conclude that abundance of food, while perhaps a factor, yet can not be said to be the controlling factor. More often, than not, the first day's hatchings were all normal, and on the second and third days the largest number of extra-bristled flies appeared. Extra-bristled flies continued to appear up to the end of the hatchings.

No record was kept of the size of the flies as there was very little difference. However, the extra bristles continued to appear in the smaller flies with seemingly the same regularity as in the larger ones. Except in large mass cultures, there was no diminishing in size at the end of the hatchings.

2. *The Influence of Temperature.*—Unlike the results from Miss Hoge's (1915) experiments, temperature did not in our cultures influence the extra bristles. Eggs put under low temperature and kept there until hatched produced relatively as many extra-bristled flies, but hatchings took a little longer. When the temperature was increased no appreciable difference was found in the bristle count. Thus, while temperature might have a slight influence, yet it can not be said to be a chief factor.

INHERITANCE

1. *Mendelian Standpoint.*—Table IX shows the ratios obtained in crosses between normals and *extras*. Two F_1 families were obtained from such matings, containing respectively 158 normals : 9 *extras* and 90 normals : 1 *extra*. These results are in accord respectively with ratios 15:1 and 63:1, which would indicate the presence of two or three equivalent factors. In the crosses made in the other three F_1 families the numbers obtained were too small for consideration here. In one case all were normals, nineteen in number. In the other two families only one or two flies hatched.

The later generations shown in table IX were obtained in every case by mating normal and *extra* sibs of the previous generation, except in the F_4 and F_5 . Unfortunately, owing to sterility and death of the *extras*, the only F_4 and F_5 cultures surviving are from collateral families. The results they give are, however, in general accord with those of the previous generations. As shown by table IX, the various ratios approximate closely in some cases to 63:1, in others to 15:1, while still other families depart widely from either of these ratios.

In comparing table X, in which in each generation *extra* sibs are mated together, with table IX, in which the corresponding matings were always between normal and *extra*, significantly different results were obtained. While in matings between normal and *extra* ratios chiefly 63:1 and 15:1, but never closely approaching 3:1, were obtained, in matings between *extras* (table X) the ratios were all

TABLE IX

NORMAL \times EXTRA MATINGS IN PAIRS

	Actual ratios	Ratios to 1	Expectation	Agreement	Conclusion
F ₁ Y	158:9	17.5:1	156.5:10.5	15:1	15:1
A	90:1	90:1	88.6:1.4	63:1	63:1
F ₂ Y ^b	101:13	7.7:1	106.9:7.1	15:1	7:1†
			93:14	7:1	
Y ^c	48:9	5.3:1	47.5:9.5	5:1	5:1
Y ^d	73:7	10.4:1	75:5	15:1	15:1
A ₂	38:5	7.6:1	37.5:5.4	7:1	7:1†
Y ⁱ	102:2	51:1	97.5:6.5	15:1	
			102.4:1.6	63:1	63:1
F ₃ Y ^b	29:2	14.5:1	29.06:1.94	15:1	15:1
Y ^c	83:4	20.7:1	81.6:5.4	15:1	15:1
Y ^d	98:4	24.5:1	95.6:6.4	15:1	15:1
Y ⁱ	51:2	25.5:1	49.7:3.3	15:1	15:1
F ₄	40:5	8:1	39.4:5.6	7:1	7:1†
	90:1	90:1	89.6:1.4	63:1	63:1
	36:2	18:1	35.6:2.4	15:1	15:1
	100:6	16.6:1	99.4:6.6	15:1	15:1
	95:1	95:1	93.5:1.5	63:1	63:1
	100:3	33.3:1	101.4:1.6	63:1	63:1
F ₅	60:3	20:1	59.1:3.9	15:1	15:1
	50:1	50:1	50.2:0.8	63:1	63:1
	80:2	40:1	80.7:1.3	63:1	63:1
	70:3	23.2:1	68.5:4.5	15:1	15:1
	50:1	50:1	50.2:0.8	63:1	63:1
	42:1	42:1	40.3:2.7	15:1	15:1

TABLE X

EXTRA \times EXTRA MATINGS IN PAIRS

	Actual ratios	Ratios to 1	Expectation	Agreement	Conclusion
F ₂ Y ^c	13:3	3.4:1	12:4	3:1	3:1
Y ⁱ	21:4	5.2:1	20.8:4.2	5:1	5:1
			23.4:1.6	15:1	
F ₃ YF	88:7	12.5:1	89.1:5.9	15:1	15:1
YE	70:5	14:1	65.6:9.4	7:1	
			70.3:4.7	15:1	15:1
YG	15:3	5:1	16.9:1.1	15:1	5:1†
			13.5:4.5	3:1	
X ₃	96:16	5.6:1	88.3:17.7	5:1	5:1
X _{3c}	46:8	5.7:1	45:9	5:1	5:1
Y _c	55:5	11:1	56.2:3.8	15:1	15:1
F ₄ A _{3c}	58:4	14.5:1	58.1:3.9	15:1	15:1
X ₄	75:10	7.5:1	74.4:10.6	7:1	7:1†
X _{4r}	16:4	5:1	15:5	3:1	3:1
F ₅ X _{4r}	33:14	2.35:1	35.2:11.8	3:1	3:1
X _{5c}	28:7	3.3:1	22.5:7.5	3:1	3:1

TABLE XI

NORMAL × NORMAL MATINGS IN PAIRS

F ₁	Actual ratios	Ratios to 1	Expectation	Agreement	Conclusion
	95:2	47.5:1	95.5:1.5	63:1	63:1
	98:5	19.6:1	96.6:6.4	15:1	15:1
	75:1	75:1	74.8:1.2	63:1	63:1
	67:0	67:0	63:1	63:1†

either 15:1 or 3:1 or intermediate, but never 63:1. On a Mendelian interpretation it would therefore appear that in matings between normals and *extras* two or three equivalent factors were always present, while in matings between *extras* there were one or two factors, but never three.

In table XI are shown the results of crossing together normal sibs in four families of the F₁ generation. The ratio of normals to *extras* is high, approximating 63:1 in three families and 15:1 in the fourth.

In tables XII, XIII and XIV the ratios of the three preceding tables are arranged serially in order to determine whether they are uniformly distributed or fall into groups corresponding to the presence of one, two or three factors. In table XII the results are indecisive, although there is a considerable gap between 10.4:1 and 14.5:1. In table XIII the results are clearer, three families falling close to 3:1, five families near 5:1 and four families near 15:1. The families of table XIV evidently group themselves similarly into two series.

TABLE XII

NORMAL × EXTRA MATINGS, SERIALY ARRANGED

Actual ratios to 1	Actual numbers	Actual ratios to 1	Actual numbers	Actual ratios to 1	Actual numbers	Actual ratios to 1	Actual ratios
5.3:1	48:9	14.5:1	29:2	20:1	60:3	40:1	80:2
7.6:1	38:5	16.6:1	100:6	21.2:1	83:4	42:1	42:1
7.7:1	101:13					50:1	50:1
8:1	40:5	17.5:1	158:9	23.3:1	70:3	50:1	50:1
				25.5:1	51:2	51:1	102:2
10.4:1	73:7	18:1	36:2	26.5:1	98:4	90:1	90:1
				33.3:1	100:3	90:1	90:1
						95:1	95:1
5:1		15:1		25:1		63:1	

TABLE XIII

EXTRA \times EXTRA MATINGS, SERIALLY ARRANGED

Actual ratios to 1	Actual numbers	Actual ratios to 1	Actual numbers	Actual ratios to 1	Actual numbers
2.35:1	33:14	5.0:1	15:3	11:1	55:5
3.2:1	23:7	5.2:1	21:4	12.5:1	88:7
3.4:1	13:3	5.6:1	90:16	14:1	70:5
		5.7:1	46:8	14.5:1	58:4
		7.5:1	75:10		
3:1		5:1		15:1	

TABLE XIV

NORMAL \times NORMAL MATINGS, SERIALLY ARRANGED

Actual ratios to 1	Actual numbers	Actual ratios to 1	Actual numbers
19.6:1	98:5	47.5:1	95:2
		75:1	75:1
15:1		63:1	

In addition to the above results of matings in pairs, it seems worth while to include the offspring of mass cultures merely to show that they give similar ratios, although these ratios cannot be further analyzed and it might be expected that some of them at least would represent the combination of offspring from unlike matings.

In table XV are shown the results of breeding together in mass culture normals which had been derived from a cross between normal and *extra*.

TABLE XV

NORMALS FROM FIRST CROSSING WITH EXTRA, BREED TO NORMALS IN MASS CULTURE THROUGH FIVE GENERATIONS

Ratios	Ratios to 1	Expectation	Agreement	Conclusion
101:13	7.5:1	99.7:14.3	7:1	7:1?
105:1	105:1	104.3:1.7	63:1	63:1
127:2	63.5:1	126.09:2.01	63:1	63:1
85:2	42.5:1	85.6:1.4	63:1	63:1
75:1	75:1	74.8:1.2	63:1	63:1
100:3	33.3:1	101.4:1.6	63:1	63:1
85:3	28.3:1	82.5:5.5	15:1	15:1

In table XVI are shown the results of breeding together in mass culture normals which had been extracted from a cross between two *extras*.

TABLE XVI

NORMALS EXTRACTED FROM EXTRA \times EXTRA AND BRED TOGETHER IN MASS
CULTURE THROUGH FIVE GENERATIONS

Ratios	Ratios to 1	Expectation	Agreement	Conclusion
101:15	6.7:1	101.5:14.5	7:1	7:1?
101:2	50.5:1	101.4:1.6	63:1	63:1
95:6	15.8:1	94.7:6.3	15:1	15:1
38:5	7.6:1	37.6:5.4	7:1	7:1?
105:1	105:1	104.3:1.7	63:1	63:1
93:1	93:1	92.5:1.5	63:1	63:1
87:1	87:1	86.6:1.4	63:1	63:1
70:5	14:1	70.3:4.7	15:1	15:1
95:1	95:1	94.5:1.5	63:1	63:1

The ratios of tables XV and XVI are rearranged in serial order in tables XVII and XVIII. It seems possible that the ratios 28.3:1, 33.3:1, and 42.5:1 in table XVII may represent combination families, since they are intermediate between 15:1 and 63:1. In table XVIII the ratios appear to be more closely grouped around 7:1, 15:1, and 63:1.

TABLE XVII

NORMAL \times NORMAL MATINGS IN MASS, SERIALLY ARRANGED

Ratios to 1	Actual numbers	Ratios to 1	Actual numbers	Ratios to 1	Actual numbers
7.8:1	101:13	28.3:1	85:3	33.3:1	100:3
				42.5:1	85:2
				63.5:1	127:2
				75:1	75:1
				105:1	105:1
7:1		15:1		63:1	

TABLE XVIII

EXTRACTED NORMAL \times NORMAL MATINGS IN MASS, SERIALLY ARRANGED

Ratios to 1	Actual numbers	Ratios to 1	Actual numbers	Ratios to 1	Actual numbers
6.7:1	101:15	14.1:1	70:5	50.5:1	101:2
7.6:1	38:5	15.8:1	95:6	87:1	87:1
				93:1	93:1
				95:1	95:1
				105:1	105:1
7:1		15:1		63:1	

Considering these results in general, the ratios 15:1 and 63:1 appear to fall in with the Mendelian equivalent-factor hypothesis. In

many families the arrangement with expectation on such an hypothesis is close, but it is not clear what significance is to be attached to the wide departures from these ratios, such as 5:1, 7:1 and 25:1. In his work on *Oenothera rubricalyx* Gates (1915) obtained similar aberrant ratios, particularly 5:1.

The ratios 15 to 1 and 63 to 1 are shown most frequently. This might, from the Mendelian standpoint, indicate that we have two or three equivalent factors for the normal condition vs. extra bristles. The triplicate condition might be thought of as resulting from similar changes in a particular locus of three chromosomes in *Drosophila*, or by matings of individuals in which different chromosomes had undergone this change. Since the inheritance is apparently not sex-linked in any case, we cannot assume that the sex chromosomes carry this factor. Similar results have been obtained by Nilsson-Ehle (1909) in wheat, by Shull (1914) in *Capsella*, and by Gates (1915) in *Oenothera*.

The fact that in the F_2 generation (table IX) the ratios are 63 to 1 and 15 to 1, representing three and two equivalent factors, seems weighty evidence in favor of the factorial theory. After the first change from the normal, one might, perhaps, expect further changes or successive mutations in the same direction as a result of crossing.

In MacDowell's (1915) extensive experiments he has postulated an inhibiting unit-factor which prevents the development of extra bristles, and accessory factors which, in the absence of the main restricting factor, produce flies with reduced numbers of extra bristles. These accessory factors are therefore different from the equivalent factors postulated in this paper, the former being used to explain the occurrence of flies with more than one or two extra bristles, while the latter is used to explain the ratios in which flies having a single extra bristle occur. In my cultures the *extra* flies, almost without exception, had only a single extra bristle. The difference in MacDowell's strain, some of which had as many as eight extra bristles, will be referred to again, but it may be pointed out here that this high-grade strain which was obtained at Woods Hole, Massachusetts, differed from all other known strains in having a number of extra bristles.

The normal condition of four bristles in most individuals is the dominant condition, yet *extra* flies appear in all my cultures. These must be judged either as new mutations, or as a result of imperfect dominance or as the expression of a heterozygous condition. Obviously,

since crosses between *extras* have given always a large majority of normals, it is impossible to speak of dominance in the ordinary sense. If we assume that one or more factors are concerned in the appearance of extra bristles, it is not necessary to resort to the idea of the loss of an inhibiting factor to explain the increased number of extra-bristled individuals in selected generations. According to the law of chance, one naturally would not expect all three or even two factors to be present in every mating. Thus we might perhaps expect to find some normals present in all cultures, even those that have been most rigorously selected. This, however, involves also the admission that the factors themselves are more or less inconstant, at least in their expression in the soma.

2. *Variation*.—From a viewpoint other than Mendelian the percentages of *extras* (tables III, IV, V, and VI) seems to indicate a fluctuating variation or sliding scale, as the percentages vary from 1.1 to 15. Additional support of this idea is found in the fact that *extras* appear in all cultures. Where normals are crossed with normals (table I, y F₂) the percentage of *extras* is 11.11, exactly the same as when *extra* is crossed with *extra* (table VII, F₄Xc), 11.11 per cent. This seems to point to the fact that we are dealing either with an ever-varying factor or with germ plasm in such unstable balance that it has a continual tendency to vary.

In the A family in the F₄ generation, five varying flies were found, three having five bristles and also two with three. We might conclude from such facts as these that the germ plasm is in an unstable condition, with a tendency to vary and to vary in either direction.

3. *Partial Inheritance*.—Instead of all flies inheriting the extra bristle, a tendency to partial inheritance was found. These intermediates had, instead of a definite extra bristle, merely a thickened hair. Such thickened hairs appeared in line with the bristle and in positions where one might expect to find an extra bristle.

TABLE XIX

RESULTS OF MATING DIFFERENT SIBS OF THE SAME FAMILIES

Family	Bottle	letter	Normals	Extras	Per cent
Y	E ²	pair	100	3	2.9
	E ³	pair	77	3	3.8
	E	mass	60	6	9.9
	E	pair	67	0	0
	E	pair	95	2	2.07
	A	pair	98	5	2.8
X	A	pair	75	1	1.3
	A	mass	85	3	2.3

Table XXII shows that whether the parent with extra bristles be male or female the extra bristles are inherited in practically the same number by both sons and daughters, thus showing that the distribution is similar in the reciprocal crosses. This is sufficient to indicate that there is no sex linkage involved, a conclusion reached also by MacDowell (1915).

In almost all cases we were dealing with only one extra bristle and the occasional two bristles were found in both males and females. Neither did there seem to be any difference in the number of bristles inherited by male and female; thus differing from MacDowell, who found a larger percentage of extra-bristled flies among the females.

SUMMARY OF EXPERIMENTS ON MENDELIAN INHERITANCE

1. From the occurrence of the ratios approximating 3 to 1, 15 to 1, and 63 to 1, we seem to be dealing with a Mendelian inheritance involving, in the various crosses, 1, 2, and 3 equivalent factors, concerned in the development of the extra bristles, or rather in their failure to appear.

2. There is also some evidence in favor of regarding this as a fluctuating variation.

3. Thickened hairs give evidence of a partial inheritance.

4. There is no sex linkage involved and extra bristles appear with the same regularity as to number and frequency in male and female.

SELECTION

Selection of normals seemed to result in a partial weeding out of *extras* in the normal cultures, but really this may have been a fluctuation since *extras* appeared in all cultures. On the other hand, a high-grade race was not obtained by the selection of *extras*. In crossing a five-bristled fly with a seven-bristled fly, a six-bristled fly with a six-bristled fly, and a four-bristled fly with a six-bristled fly, the same results were obtained.

TABLE XXIII

COMPARING NUMBER OF EXTRA BRISTLES IN PARENTS AND OFFSPRING

	Number of bristles in parents	Normal
$5 \times 7 = 6$ extra-bristled flies, 5 flies with 5 bristles, 1 fly with 6 bristles		55
$6 \times 6 = 8$ extra-bristled flies, 8 flies with 5 bristles		46
$4 \times 6 = 4$ extra-bristled flies, 4 flies with 5 bristles		83
$6 \times 5 = 5$ extra-bristled flies, 5 flies with 5 bristles		70

Thus selection seems to have no influence on the inheritance of an increased number of extra bristles in this strain. Six-bristled flies occurred in crosses with normals and *extras*, and even in crosses of two normals.

Selection did not increase the number of *extras* appearing in high-grade families, namely in families resulting from crosses of *extra* with *extra*.

TABLE XXIV

COMPARING NUMBER OF EXTRAS IN LOW GRADE AND HIGH GRADE FAMILIES

Family	Normals	Extras	Per cent	Family	Normals	Extras	Per cent
X	85	3	3.4	A ₅	93	1	1.05
Y	106	1	0.94	X ₅	90	6	5.8
A	98	3	2.9				

Extras appear with varying frequency both in the first cross of normal with *extra* and in crosses with later selected generations, as shown by table XXV.

TABLE XXV

SHOWING VARIATIONS IN PERCENTAGE OF EXTRAS

			Normals	Extras	Per cent
F ₁ Y	extra ♀	normal ♂	158	9	5.32
F ₁ Y _r	extra ♀	normal ♂	62	1	1.61
F ₁ A	extra ♂	normal ♀	90	1	1.11
F ₁ A	extra ♀	normal ♂	70	3	4.1
X	extra ♂	normal ♀	95	1	1.03
F ₃ X ₅	extra ♀	normal ♂	106	6	5.66

If selection was a factor in the appearance of extra bristles, when two *extras* were mated and the extracted normals crossed, one might expect the greater number of extra-bristled flies to appear in the extracted culture, rather than in the normal culture. Such is not the case, however, as *extras* appear with equal frequency in normal culture and in extracted normal cultures from mating of two *extras*.

Nor. from extracted F₃X₅ 101 Nor. bred in mass = F₄X₅ = 101 Nor. + 2 ex. = 1.94 per cent.

Nor. from normal F₂Y 127 Nor. bred in mass = F₃Y = 82 Nor. + 3 ex. = 3.32 per cent.

In high-grade cultures where *extras* have been bred with *extras* for successive generations, one might expect to find a higher frequency of extra bristles appearing in subsequent generations than in cultures where two *extras* descended from normals were bred together. This

is not true, however. F_4X_a descended from normal = 86 N. + 10 ex. = 11.6 per cent. $F_4X_{c_1}$ descended from extra crosses = 44 N. + 5 ex. = 8.1 per cent.

SUMMARY OF EXPERIMENTS ON SELECTION

1. Selection for an increased number of extra bristles makes no advance, the tendency being to return to the conditions of four and five bristles.

2. High-grade parents do not produce high-grade children, in fact there is no definite relation between parent and offspring as to the number of extra bristles.

DISCUSSION

Certain of the data seem to point to the fact that we are dealing with a Mendelian inheritance and that three factors are concerned, giving frequently the 63 to 1 ratio rather than the simple Mendelian ratio of three to 1. The results here agree with the work of Nilsson-Ehle (1909), Shull (1914), and Gates (1915). The intermediate ratios, 5 to 1, 7 to 1, and others, might be explained either by fluctuation or alternating dominance. The latter is easily conceivable as shown in the fluctuating percentages of *extras* in tables III, IV, V, and VI. If the dominance of normal were complete, there would have been more regularity in the percentages. Some of the departures from expectation are of course not mathematically significant, but the various standard deviations have not been worked out.

The fact that some of the results are so different from those of MacDowell (1915), as for instance, the failure to develop a line producing practically all *extras*, may be partially explained by the fact that he was dealing with eleven generations and in this case we have only five. Nevertheless, results were different from the beginning and it seems necessary to find some other explanation than that of the loss of restrictive or inhibiting factors.

The fact that the family having the greatest number of *extras*, the Y family, also had the greatest number of other mutations or variations, namely, the club-wing mutant, the beaded wings, the abdominal variations and the fly with only one wing, seemed to point to the facts that there were other factors involved and that the germ plasm was in an unstable condition. The increase of sterility among the extra-bristled flies and the fact that they were not so viable may

also have some influence on the factor or factors involved; or it may simply be in agreement with Stark's (1915) work showing the increased occurrence of lethal factors in inbred stock. In that case there should be the same results in normals, as they were also inbred. Hyde's (1914) conclusions do not seem to have any bearing on the results found. The sterile females in his experiments contained eggs, but these were not laid, apparently owing to an obstruction in the oviduct. In all cases examined in my cultures, however, no eggs were found in sterile females.

The results of selection only in part agree with the work of Zeleny and Mattoon (1915). They disagree in that selection does not increase the mean number, but agree in that the individuals in any generation differ as regards germinal constitution. Also the conclusion is the same, namely, that probably other factors were concerned, or the variability is due to the presence of original differences in factorial composition, rather than to the addition of new ones or the loss of any factor.

Selection of extra bristles did not result in the establishment of a pure line as by Lutz (1911) in his experiments in selection of abnormal venation of the wings of *Drosophila*. Nor do our results in selection compare with Dexter's (1914) results in selection on beaded stock. He established a line which bred practically pure. However, if unselected it returned to the normal condition. Results similar to those of Lutz were obtained as regards *position* of inheritance, namely, that there was no relation of offspring to parent in regard to the position of inheritance. As in the case of Tower's (1906) experiments on *Leptinotarsa*, if selection was stopped the flies returned to the normal mean.

Lethal factors, while probably present, yet seemed to have no influence on the sex ratios, but the fact that the *extras* were less viable might support the theory of Liff (1915) in his paper on a peculiar Mendelian ratio. He was working with a pink-eyed mutant and the peculiar ratios were found to be due to lethal factors. Morgan has done extensive work with lethal factors appearing in *Drosophila*. Perhaps in this case the lethal factor was introduced by both extra-determining chromosomes, and that is why in the hatching we have such small numbers.

It is not possible from the results to decide finally either in favor of a Mendelian interpretation or of a fluctuating variation, as neither explanation is completely satisfactory.

The ratios 3 to 1, 15 to 1, and 63 to 1, point to a Mendelian inheritance, but the ratios 5 to 1, 7 to 1, and others are at present unexplainable. They may have some significance as such or they may merely be intermediates in a continuous series. The latter seems improbable, however, on account of the closeness of many ratios to Mendelian expectations. Perhaps some explanation will be found to make the other ratios understandable.

CONCLUSIONS

1. We may be dealing with a case of Mendelian inheritance in which one, two, and three equivalent factors are concerned. However, there are various facts which this interpretation does not explain and for the explanation of other ratios obtained it seems necessary to assume also, in certain cases, fluctuating variation or alternating dominance. Other hypotheses might also, of course, be formulated to account for the results, but it does not appear worth while to discuss these in the present state of the problem. Data showing the linkages of the factor or factors for extra bristles with other factors appear to afford the most probable basis for a solution of the question.

2. There seems to be a partial inheritance or intermediate condition, as shown by the occasional occurrence of thickened hairs.

3. In accord with the results of MacDowell (1915), the inheritance of extra bristles is found not to be sex-linked.

4. Selection does not increase the number of bristles in extra-bristled individuals, nor does it give a pure line.

5. There are more extra-bristled flies appearing in crosses between *extra* \times *extra* than between *extra* \times normal. The ratio 63:1 was never obtained in *extra* \times *extra*, and the ratio 3:1 never occurred in normal \times *extra*.

6. The amount of food does not appear to influence the number of extra bristles, as they appear all through the hatchings.

7. *Extras* appear with equal frequency in low-grade and high-grade cultures when *extra* is crossed with normal.

8. Temperature plays no important part in the development of extra bristles.

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ERRATA

- Page 36, line 5 from bottom. *For asiastica read asiatica.*
Page 49, line 4. *For Cysloposthium read Cycloposthium.*
Page 381, line 29. *For Frigillidae read Fringillidae.*
Page 389, line 8 from bottom. *For Galibulidae read Galbulidae.*
Page 442, line 5. *For rubra read ruber.*
Page 449, line 23. *For Lepus europaeus read Oryctolagus cuniculus.*

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